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U. S. DEPARTMENT OF AGRICULTURE
BUREAU OF ENTOMOLOGY AND PLANT QUARANTINE
FOREST INSECT INVESTIGATIONS

SUMMARY OF INVESTIGATIVE AND CONTROL WORK ON THE MOUNTAIN PINE BEETLE
IN SUGAR PINE STANDS OF CALIFORNIA

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1945

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May 15, 1945

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SUMMARY OF INVESTIGATIVE AND CONTROL WORK ON THE MOUNTAIN PINE BEETLE
IN SUGAR PINE STANDS OF CALIFORNIA
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G. R. Struble

INTRODUCTION

Investigative and control work dealing with the mountain pine beetle within California sugar pine stands has continued for a number of years by the Berkeley Office of the Division of Forest Insect Investigations, Bureau of Entomology and Plant Quarantine. Resulting therefrom are numerous reports and manuscripts, and some publications on different phases of this problem. These writings are concerned principally with seasonal history and habits, the relationship of the beetle to this host, the extent and character of its damage, the practice and results of direct control by the fell-peel-burn method, and the development of control methods.

A summary of the information contained within these reports is desirable for several reasons. There is much need for the simplification of the detail contained within them. The organization of subject material into readily available form is advantageous as a time saving factor for those seeking a perspective on the problem. Much work is still to be done before the best means of controlling the beetle is determined, and this summary will be of benefit to the researcher as a background of information and guide to further effort. It is aimed to point the way toward renewed effort along the lines holding the greatest promise of solution.

Additional details on the habits of the mountain pine beetle as a primary insect in lodgepole pine and western white pine are available in many reports written about these problems in the northern Rocky Mountain region. The behavior of this insect in these hosts and others that it attacks is similar in many ways to its habits in sugar pine. For this reason, frequent reference to information on the habits and life history in reports pertaining to lodgepole or white pine will be made when such information is lacking from sugar pine.

IMPORTANCE OF MOUNTAIN PINE BEETLE IN SUGAR PINE

There are approximately 3,500,000 acres within the California pine region in which sugar pine is considered a type species. Much of the virgin stumpage has been cut, but there are still over 20,000,000,000 board feet left, most of which is of excellent quality. Compared to ponderosa pine and Jeffrey pine with slightly less than 50,000,000,000 board feet in virgin stumpage, sugar pine is still a major timber species in this state.

These virgin sugar pine stands are subjected to severe beetle damage. The mountain pine beetle is the principal insect agency of destruction, and is responsible for the death and complete waste of valuable stumpage every year. Periodically the populations of this insect increase and cause many times the normal number of trees to be killed. In most cases there is little possibility of salvaging these trees for lumber; butt logs are frequently utilized for shakes, but aside from this use most of the trees killed are a total loss from the commercial point of view.

Some conception of the destruction caused is gained from the insect control records. For example, between 1913 and 1939 nearly 6,000 trees having a total volume of 25,500,000 board feet were treated in the southern Sierra forests from the Stanislaus to Sequoia National Forest at a cost of nearly \$100,000. This probably represents less than 10 percent of the total losses caused by the mountain pine beetle for these areas alone during this period. Furthermore, the areas on which this control work was undertaken is less than 10 percent of the total sugar pine acreage in California.

HISTORICAL REVIEW

A. D. Hopkins' (8) account in 1899 of a "special and dangerous enemy of the sugar pine and the mountain white pine" is the first record of Dendroctonus damage to these trees. From the additional notes of damage to sugar pine, lodgepole pine, and western white pine by Hopkins in 1902 and 1904; J. L. Webb in 1900 and 1905; and by H. E. Burke from 1904 to 1907, the identity of the mountain pine beetle, its habits and its relation to heavy timber losses were well established. It was named D. monticolae by Hopkins in 1909 (9). The initial attempt to control the mountain pine beetle was concerned with lodgepole pine infestations. According to Craighead, et al (1a): "The first effort to control an outbreak of the mountain pine beetle in lodgepole pine was made in 1910 and 1911 on the Whitman National Forest in northeastern Oregon."

F. P. Keen's (60) experiments in 1916 on host tree selection in ponderosa pine and sugar pine, and his observations on the feeding habits of the mountain pine beetle in sugar pine (61) were the only investigations directly concerned with the sugar pine host until 1932. Closer attention was given to the lodgepole pine problem in which the seasonal history and many of the habits of the beetle were worked out by J. E. Patterson (72) in 1917 from infestations in Yosemite National Park, California. This work was followed by studies and experiments in lodgepole pine by Patterson, Evenden, and Gibson from infestations in Oregon, Idaho, and Montana. Studies of the infestations and habits of the beetle in western white pine by DeLeon, Bedard and Gibson were undertaken in the northern Rocky Mountain region from 1930 to 1940. Detailed investigations of the seasonal history and habits of this beetle, and studies of host relationship in sugar pine have been continued by the writer since 1932.

Control of the mountain pine beetle in sugar pine by felling and removing the bark from the infested bole was advocated by Hopkins in 1909 (9), but this method was never extensively used. The first control attempts on a project basis were undertaken in 1913 and 1914 in conjunction with the control of the western pine beetle in ponderosa pine (Chiquito Basin, Sierra National Forest) by felling, peeling and burning. In all major control projects since then (White & Friant cooperative--Sand and Whiskey Creek, 1924; San Joaquin project, 1919 to 1924; Stanislaus, Yosemite, Sierra projects 1931-1935) the fell-peel-burn method was used with much success in reducing infestations. Efforts to improve on methods of control and reduce the fire hazard have not as yet been fully as effective as the burning method. The use of toxic penetrating oils, fumigating gases, chemicals injected in the sap stream, etc., have been only partially effective. Studies were also undertaken to determine the effectiveness and importance of native insect predators. The most recent development has been an attempt to identify trees that are susceptible to beetle attacks.

SEASONAL HISTORY AND HABITS

The Adult Beetle

Description.

The original description, made by Hopkins (9), is as follows: "The mountain pine beetle is a stout, black, cylindrical bark beetle 3.7 to 6.4 mm. long, having the head broad, without frontal groove, but with a short longitudinal impression above the middle."

The adults have been variously described by Swaine (24), DeLeon (42), Doane et al (5), Keen (14), and Evenden et al (7); but with little improvement on the original description. All agree that it is a "stout, black, cylindrical bark beetle," that its length varies, and that in the immature stages the color is yellowish to brown.

Food habits.

The adult most probably derives its nourishment from particles of phloem or cambium as it bores through these tissues during the excavation of egg galleries. While details on this subject are lacking from various reports, it is generally implied that the phloem, which is a rich source of sugars and starches serves to sustain the adult during its life period. Repeated dissections by the writer of the adult alimentary tract have revealed the presence of phloem tissue, and it may be presumed that nourishment is taken from this material. Much of the boring by adults is through the corky outer bark, and while this material has been observed in the alimentary tracts, it is doubtful if a great deal of nourishment is derived from it. In boring exit holes, and in boring through the corky outer bark prior to the establishment of egg galleries, most of the particles bitten off by the beetles are believed to be cast aside.

Mating Habits.

The mating of adults has never been observed in sugar pine, but it probably occurs most often in the egg galleries at intervals during excavation. Evenden et al (7) state that "Fertilization occurs after the heavy flow of pitch has stopped, which is usually when 1 or 2 inches of egg gallery have been excavated. After mating, the males may leave the tree, possibly to seek new mates." In western white pine, Bedard (27) states that "Mating takes place in the newly constructed gallery after the attack has started." Patterson (73) observed mating to take place on the outside of the bark of lodgepole pine as follows: "Presently the female started to attack in a slight crevice of bark; in a minute or so she had penetrated the bark until her head had entirely disappeared, at this stage the male approached quite closely and for a few minutes the pair appeared to be in copulation." DeLeon (38) recorded an observation made by Gibson and Rust from lodgepole pine in 1927 in which a male beetle was seen to "copulate with a female at the entrance of the gallery. The male after copulation wandered off, inspected other galleries, and finally apparently tried to induce another insect to copulate."

Sex Ratio.

No record has been made other than notes by the writer on the sex ratio of emerging new adults from sugar pine. These notes indicate that the proportion of males and females is approximately equal.

Considerably more information on the sex ratio of emerging adults is contained within reports written about the mountain pine beetle in western white pine. Bedard (27) concluded as a result of examinations made on 1,000 emerging adults that "There is an equal number of males and females when the young adults emerge from the trees - -." DeLeon et al (2) found "by examining 2,500 new adult beetles taken from new broods ready for emergence, that male and female beetles are present in equal numbers before they emerge from the brood trees and make their initial attack."

The sex ratio of attacking beetles in sugar pine has not been investigated, but in western white pine DeLeon (38) and Bedard (29) found that the sex ratio in newly attacked western white pine is 2 males to every 3 females. DeLeon et al (2) state "an examination of 4,010 adults taken from the egg galleries in newly attacked trees showed that 60.8 percent were females and 39.2 percent males." They further state that "the inequality of sexes in the new attacks is due to the fact that many males die in the egg galleries after the first attack."

Method of Attack.

Studies by Struble (99) revealed that the initial attacks made by the adult beetle on mature sugar pine usually occur in the upper half or third of the main stem; in smaller trees (under 30 inches D.B.H.), and frequently in some of the larger trees, concerted attacks occur over the entire length of bole

from within a few feet of the top to within 3 to 10 feet from the ground. Trees with initial infestations in the upper part of the stem are attacked in the mid-bole and basal portion of the bole by succeeding flights of beetles. Struble (99) states that "during the flight period no great number of adults are found at one time, but within a period of a few days after a tree has been selected, many beetles are found in the process of constructing the characteristic pitch tubes on the outside of the bark."

Repeated observations by the writer, but not recorded, have revealed that the beetle in making its attacks on sugar pine prefers a bark crevice or depression in which to begin excavation. After a definite location is decided upon the beetle bores continuously, biting off bits of outer bark and casting them aside. Considerable rotation of the body about the newly founded entrance is a characteristic habit as the beetle bores its way inward.

The number of attacks occurring per unit of bark area is variable. The average number found in 36 square feet of sugar pine bark examined by Struble (99) in 1933 was 6.8 per square foot. Additional records in the notes of the writer taken during 1939 from 43 square feet of bark area from 14 infested trees was 8 attacks per square foot with variations from 4 to 20 per square foot. In lodgepole pine Patterson (77) found an average number of 7.25 attacks per square foot from 1,676 square feet of bark area examined. According to Bedard (31) working in western white pine "it is apparent that the greatest efficiency in gallery construction is secured when there are 9 to 15 attacks per square foot."

Construction of the Galleries.

Reports concerning the attacks and excavation of egg galleries all indicate that the female adult is responsible for most of the work. Keen (61) reporting from observations in sugar pine in southern Oregon during 1916 states: "The female commences the construction of the gallery, and does all of the construction work at the head of the gallery, while the male fellows behind and assists by desposing of frass." Struble (99) observed from studies in sugar pine in the Yosemite area during 1933 that "males have often been found excavating the so-called 'ventilation holes'." Patterson (73) observed from studies of this beetle in lodgepole pine in Yosemite National Park during 1917 that "the females appeared to enter the bark first and start the brood galleries; later, as the galleries were being constructed, the females were found at the terminal ends doing the actual excavating." The role of the sexes is more clearly depicted by Evenden et al (7) who state: "Attacks are initiated by female beetles which bore through the bark and excavate the egg galleries beneath. During the construction of the entrance holes, the male beetles are attracted to the trees and follow the females as the tunnels progress. As pitch flows from the wounded living tissue of the tree, the male keeps the entrance hole free of this resin and the boring frass, thus forming the pitch tube on the bark surface. - - The males are obliged to pack the frass into the tunnel as it is made by the female to avoid being surrounded by it."

The egg galleries are described by Hopkins (10) as "longitudinal, distinctly to slightly winding or straight, usually grooved on the surface of the wood and deeply grooved in the bark." The tendency of the galleries to wind is particularly characteristic in sugar pine. Struble (99) described these galleries as follows: "They extend vertically as a rule, but do not always run true to form, for they are commonly found winding to and fro without definite pattern. The more typical gallery is curved at the bottom for about 2 or 3 inches and runs vertically from the curve to 24-30 inches when complete." Keen (14) states that "the galleries may be nearly straight or slightly sinuous, and sometimes, particularly in sugar pine, decidedly winding, and at the bottom of these galleries there is a short crook or bend 1 or 2 inches in length. The perpendicular portion of the gallery ranges in length from 12 to 36 inches and nearly always follows the grain of the wood."

Egg Laying.

The adult female deposits its eggs singly in niches excavated along each side of the egg gallery, beginning within 2 to 3 inches of the entrance. According to Struble (99) "small indentations or pockets are made at irregular intervals along each side of the gallery. In each pocket from 1 to 4 eggs are deposited singly in individual niches. Following each deposition, frass material is packed tightly behind the egg." Keen (14) states that the "egg niches occur on alternate sides during the construction of the egg gallery."

The number of eggs deposited by a single female adult is variable. Struble (99) found as a result of examinations made on 964 inches of egg gallery in sugar pine that there were 3,168 eggs. The average number per inch was 2.61 with a variation of 1.14 to 4.81 to the inch. An examination of 100 egg galleries in lodgepole pine in southern Oregon by Patterson (77) revealed that there were 6,971 eggs which averaged 69.7 per gallery. He found a variation of from 33 eggs in 21 inches of gallery to 149 eggs in 12 inches of gallery. Bedard (31) found as a result of examinations made on 241 galleries in western white pine that there was a "variation from 4.5 to 5.5 eggs per inch up to the first 10 inches," and a distinct drop in the number per inch beyond 11 inches. He concludes "thus, an egg gallery from 10 to 12 inches long represents the optimum because it is the maximum in efficiency."

Life Span.

The life span of the adult is variable, depending principally on temperature, available food and moisture. At temperatures above 90° F the life span is presumably shortened because of intensified metabolic activity, but no information on this point is available. At temperatures under 50° F the metabolic activity is slowed down so that, even without food, the mortality rate of the adult is very low. For example, the mortality of 125 adults stored in a refrigerator at 40° F for 30 days in 1943 (Struble's notes) amounted to only 16 percent.

Without food and moisture at normal temperatures (65° F to 85° F) for beetle activity, the mortality rate is very high within a short period. For example, the mortality rate of 1,038 adults stored at normal temperatures in total

darkness during 1943 (Struble's notes) varied from 26 percent at 4 days, to 50 percent at 6 days and to 100 percent at 12 days. Keen (61) found that 28 days was the longest period of survival for adults in storage without food.

In the normal habitat of the beetle the longevity during the summer is probably between 40 and 60 days on the average, although this point has not been thoroughly checked. Adults attacking during the fall, hibernate during the winter, and resume activity during the spring; hence their life span is increased considerably, primarily as a result of lowered temperature conditions. The longest record of adult life was reported by Keen (61) who found an adult still alive 245 days after attacks were established on a sugar pine in southern Oregon.

Parent Adult Emergence.

The emergence of adults after a period following the initial attacks on a given tree and their re-attack on another tree is a common habit of this beetle, and in some host species is considered an important factor in the upbuilding of populations. It is probably not as important in sugar pine as in some of the other host trees, as indicated from Struble's (99) observation that "only a small proportion of the adults emerged, following a five-week period of attack, and no difference was found at the termination of an experiment after two months." In notes recorded by Struble in 1938, parent adult emergence from sugar pine logs under controlled rearing conditions amounted to between 11 and 15 percent of the number of beetles introduced originally. Evenden et al (7) state: "The extent to which this habit occurs varies considerably among different host trees. For example, only 10 to 30 percent of the parent adults emerge from infested sugar pine, while from western white pine nearly all of them emerge and re-attack."

The reports of DeLeon (38), Bedard (31) and Gibson (48) all indicate that the emergence and re-attack habit in western white pine includes a high proportion of the adults. For example, Gibson (48) estimated as a result of examining 117 square feet of bark from 13 infested trees that "more than 90 percent of the parent beetles emerged." Bedard (31) states as a result of one study in 1936 "that the number of parent emergence holes is almost equal to the number of attacks in the early trees, slightly more than half the number of attacks in the mid-season trees, and less than half in the late trees." DeLeon et al (2) conclude: "From these studies it can be stated that mountain pine beetle adults attacking western white pine emerge from the trees after making one attack and enter other green trees to make a second attack. It is obvious, therefore, that the rate of increase of any infestation is nearly twice as great as was formerly believed, and that the potential danger of any infested material overlooked in control is approximately doubled.

Parent adult emergence takes place after a period of 3 to 5 weeks following the initial attack. DeLeon (38) states that "emergence begins with a few beetles leaving the tree about 20 days after attack and only a few more leaving each succeeding day until suddenly a relatively great number emerge

over a space of one or two days, and after that there is a fairly rapid tapering off of emergence. The period from attack to peak of emergence, which is generally between 28 and 31 days, appears to be much more constant."

The Egg

Description.

The eggs of the genus Dendroctonus were described by Hopkins (10) as follows: "short, oval to oblong-oval, pearly white and shining, and apparently without sculpture and specific characters, except in relative size, corresponding with the size of adult representatives of the species." This is the only description to be found anywhere in the literature, either published or unpublished. Generally, it suffices for D. monticolae eggs. The approximate size of these eggs is 1 mm. long and $\frac{1}{2}$ to $\frac{3}{4}$ mm wide.

Incubation Period.

The period required from the time eggs are deposited until they hatch is variable, depending evidently for the most part on prevailing temperatures. In sugar pine Struble (99, 116) reported periods varying from 5 to 12 days. He states as a result of close records on 25 trees (99) that the average period for eggs deposited in the fall among broods which overwinter is 12 days, and for those deposited in the summer is 9 days. Under laboratory conditions where temperatures were more constant the period varied from 5 to 7 days. In lodgepole pine in the Yosemite area, Patterson (73) noted that "the first eggs were deposited in the first galleries started approximately 14 days after attack (August 14). The first larvae appeared on August 28; therefore the incubation lasted approximately 14 days."

The Larva

Description.

The generic description of Dendroctonus larvae was given in 1909 by Hopkins (10), but no generic or specific descriptions have since then been added in the various reports, manuscripts, and publications on the mountain pine beetle. His description of the characteristics of the genus is as follows: "The body of a matured larva is cylindrical, deeply wrinkled, legless, and with a few long hairs on each segment, becoming longer on the posterior ones. The head is moderately large, shining, yellowish, and with a few hairs on the scutellar lobes. Front distinct; antennae present, but obscure; eye spots not present. The thoracic segments are larger and more prominent in some species than in others. Abdominal segments 1 to 9 are of about equal width and length; 10 is represented by the anal lobe."

Feeding Habits.

According to Struble (99) the larvae begin feeding immediately after hatching from the egg. He states that they feed individually "in small channels at right angles to the egg gallery, the channels increasing in size with

larval growth and development. Most of the brood in this stage spends the entire feeding period along the inner phloem layer next to the wood. Individuals occasionally mine for a distance into the bark, this factor apparently depending on bark thickness and available food supply. When mature, each larva hollows out a cell, usually between the bark and wood, where it remains in a quiescent state to complete the prepupal and pupal stages."

Number of Instars.

The only record of the number of larval instars is contained in a laboratory memorandum written by Struble (108) in 1937. This record was determined as a result of head capsule measurements made on 420 larvae. He states that "while the total number of larvae measured is perhaps insufficient to conclude without question that there are 4 larval instars, the groupings are distinct and the frequency in each group is often enough for a tentative conclusion to this effect."

Development Period.

The development period of the larva from the newly hatched egg to the pupal stage is variable, and this is dependent on temperature conditions, food, and moisture supply. At room temperatures (70° F) Struble (108) found that the period of each instar of larvae reared on phloem inside glass tubes was as follows: first instar - 5 days; second instar - 6 days; third instar - 4 days; fourth instar - 16 days; total period - 31 days. Under field conditions during 1933, Struble (99) found as a result of close records from 25 sugar pines that the average development period in days for larvae which overwintered was 260 days, whereas the average period required for the development of summer broods was 33 days.

The Pupa

The pupa of the genus Dendroctonus is described by Hopkins (10) as follows: "The pupa is of the general size of the adult, and is distinguished by its broad prominent head, and the form of the prothorax. The sculpture and armature vary with the age of the specimen. In the pre-imaginal stage the granules and spines become more obscure." A few additional notes on D. monticolae pupae are contained within Hopkins' (10) statement that "In addition to the generic, divisional, and sub-divisional characters, the apex of the front and middle femora is armed with two small apical spines." No other descriptions are contained in reports or publications on this stage of development.

The duration of the pupal stage is generally short, and variations in the period required for the adult to issue are apparently dependent on temperature conditions. Struble (99) found as a result of records taken from 25 trees that the period varied from 9 to 12 days, with the shortest period during the summer. DeLeon (42) states that "The pupal period averages close to 10 days and is passed in a cell generally constructed between the wood and the

bark, but occasionally entirely concealed in the bark." According to Keen (14) the "pupal cells are usually exposed when the bark is removed but in thick-bark trees they may be concealed in the inner bark."

The period between the issuance of the new adult from the pupa and emergence varies considerably. DeLeon (42) sums up the habits of the new adults in sugar pine well in his statement that "after transforming, the new adults chew around under the bark, apparently feeding on the soft inner dead bark for varying periods of time before emerging. Some beetles emerge almost as soon as their body structure becomes hardened, though the beetle may still be light brown in color. Other beetles remain under the bark a considerable period even after they are jet black." Keen (14) states "The new adults may bore away the intervening bark between pupal cells and congregate beneath the bark prior to emergence, or individual emergence holes may be constructed directly from the pupal cells. Two or more insects often use the same emergence hole and the emerging beetles often take advantage of cracks in the bark or holes resulting from woodpecker work."

Seasonal History

Number of generations.

The number of annual generations produced in sugar pine is dependent on the temperatures prevailing within the range of this tree. The main body of commercial sugar pine extends from the 36th to the 42d parallel of latitude. Keen (61) reporting from the northerly limits found that "the maximum number of generations annually is one and a partial second." Struble (99) reporting from areas lying between the 26th and 38th parallel states that "two complete generations are produced each year by the mountain pine beetle in sugar pine stands found in the central Sierra region. A partial third generation is frequently produced if warm spring and fall conditions prevail." Within the intermediate latitudes there are probably 2 generations per year. The number of generations is subject to some variation even in the same degree of latitude, owing to local conditions of temperature. Evenden et al (7) state "in southern Oregon and California there are 2 complete generations annually, and a partial third in years when activity begins unusually early in the spring. Attacks initiated in March, April, or May by overwintering adults result frequently in the production of 2 complete summer generations and the beginning of a third."

In other pine species Patterson (77) working in lodgepole pine in southern Oregon reported that there was one complete generation each year at elevations ranging from 5,500 to 6,200 feet, latitude 43° N. In the northern Rocky Mountains, Bedard (29) found that "the mountain pine beetle in western white pine has, therefore, two broods, one and a partial second generation instead of the one brood, one and a partial second generation heretofore believed."

Overlapping of Generations.

Broods varying in age from eggs to new adults may be found at any time from spring to fall within the sugar pine belt. The overwintering stages are composed of eggs, larvae varying from first stage to fully grown, new adults varying from callow to black, and parent adults. With the advent of developmental temperatures in the spring, more eggs are laid by overwintering parent adults, new attacks are initiated by new black adults emerging, the larvae begin feeding, and the oldest of them pupate. Struble (99) states that "adults are found in flight on warm days at any time from March 15 to November 15, but in large numbers only during late June, July and early August when the main summer attack is made. Attacks occur constantly throughout the flight period, and a great deal of variation in brood stages is found at any time during the year." The flight period of adults emerging from the main summer generation begins late in August and continues through September, October and part of November, depending on the seasonal temperature conditions.

The overlap of generations and broods is just as prevalent in other host trees attacked by the mountain pine beetle. In western white pine Gibson (48) found that "attacks of the mountain pine beetle in western white pine are extended over a long period each summer. A few which overwinter as new adults emerge and make an initial attack in June, after which there are no apparent attacks until July when the main attack begins and continues until September or possibly even later." Bedard (29), also working with this beetle in western white pine, reports that "in the early spring before insect activity begins, three distinct overwintering brood stages are to be found in the western white pine region of northern Idaho and eastern Washington. A survey of 275 infested trees showed that 24.4 percent contained small larvae and overwintering parent adults, 25.1 percent contained new adult beetles, and 50.5 percent contained mostly mature larvae."

Number of broods.

According to Struble's (99) life history chart (Figure 2), there are 2 distinct main flight and attack periods each year; one from the middle of June to the first of August and the other from the middle of August to the middle of November. The first flight period originates from the overwintering broods of larvae in varying stages produced from September to November. The second flight period originates from broods of the summer generation which begin emerging about the middle of August. From these attacks there are developed 2 distinct broods which overlap to a considerable extent. A third and fourth partial attack period occurs either early in the spring or late in the fall or both, depending on seasonal temperature conditions, and these result in broods which overlap with the others. It is therefore possible for the mountain pine beetle in sugar pine in the central Sierras to have 4 broods per year. In addition there are also broods produced by the re-emergence of parent adults, but broods from this source are believed to be relatively small.

The effect of altitude on the number of broods or rate of development under similar conditions of exposure is apparently of little importance, according to Struble's (99) observations from 2 trees in which attacks were induced on them through caging. Struble reports that "cage 21 was situated at approximately 4,200 feet, while cage 23 was built around a tree at 7,000 feet elevation. Both elevations represent the extremes of the sugar pine range on the Sierra National Forest. - - Thermograph records of air temperatures were taken from each situation during the entire period of development. - - Daily maximum and minimum temperatures taken from these records - - show from 10 to 15 degrees difference under each situation." Table IX (same report) showed no appreciable difference in development under each condition. The explanation for this lay in the number of hours within the developmental temperature range of this insect. Struble states that "temperatures between 50 and 70° F are evidently most important, since in each case the number of hours exposure is nearly equal."

Overwintering.

Both Keen (61) and Struble (99) indicate that the winter is passed by the mountain pine beetle in sugar pine in all stages of development. Keen, writing from studies conducted in southern Oregon, states "D. monticolae has been found overwintering in all stages. On the Lamb's Mine unit it is principally found as parent adults, with eggs and young larvae, also new adults and pupae." From the Sierra National Forest in California, Struble reports that "the overwintering brood stages occur in all ages of larvae, pupae and new adults."

A modification to the above conception of the stages passing the winter is contained in Keen's (14) statement that "the winter is passed in all stages of development except that of the pupa." Judging from later observations of the writer, and not recorded in his notes, it is probably true that pupae do not overwinter. Pupae have been found, even as late as the fore part of January, but it is believed that they develop to adults within a short period and pass the remaining part of the winter in the adult stage. Generally the temperatures from December 15 to March 1 are believed to be too low to induce pupation.

In laboratory tests with mountain pine beetle larvae and pupae to determine the effect of lowered temperatures on development, Whiteside (121a) demonstrated that temperatures below 50° F. definitely limited development beyond the larval stage if the prepupal condition had not been attained. He stated:

"Larvae in the prepupal condition transformed to pupae and to callow adults at temperatures from 74 to 50° F. At 45 and 41° F larvae in this condition reached the pupal stage but were killed by fungi. At 36 and 32° F. no development occurred

"Callow adults appeared from early pupae (all white) at temperatures as low as 41° F. At 36° F. the pupae were unable to break the pupal skin and did not become perfect adults. At 32° F. none developed. Pupae that were more advanced (showing body color) reached the callow adult stage at temperatures as low as 36° F. One transformed at 32° F. but was probably more advanced than the others.

"At 50° F. the development (of larvae) progressed at a much slower rate and only a few reached the callow adult stage. Below 50° F. practically no development has taken place after 120 days of continuous exposure. There were 2 pupae appearing at 45° F. after 32 days' exposure, probably from larvae near the prepupal stage at the time they were placed."

As a result of this study, Whiteside concluded:

- (1) "For practical purposes the zero of development for larvae appears to be close to 50° F.
- (2) "It appears that the change from the mature larval to the prepupal condition acts as a bar to pupation at lower temperatures.
- (3) "That once this bar is broken the transformation to the pupa and adult stages will continue at temperatures as low as 36° F."

Mortality during Life Cycle.

No studies have been undertaken in sugar pine to determine the amount of mortality that occurs throughout the life cycle of the mountain pine beetle. The best estimate may be determined by the ratio of biotic potential to emergence. The average length of egg galleries per square foot among normally attacked trees is approximately 100 inches (average of 4,263 inches of gallery from 44 square feet of bark from 15 overwintering trees, 1939-1940). The average number of eggs laid per inch of gallery is about 2150. The average number of emerging adults lies somewhere between 20 and 40 per square foot of infested bark. The mortality during the life cycle, therefore, is estimated between 85 and 95 percent.

The mortality of the mountain pine beetle in western white pine from egg to adult is estimated by Bedard (31, 32) at "approximately 90 percent." He states (32) that "the greatest mortality is suffered in the egg stage, probably as a result of predaceous mites and unfavorable temperature and moisture conditions. Much of the mortality in all stages occurs during the winter months." He concludes: (34) "Obviously there are factors at work, the sum total of which is called environmental resistance, which prevent the potential increase from becoming actual."

Effect on Infested Tree

Condition of Tree at Time of Attack.

There is no evident relation between the outward appearance of a sugar pine tree and its chances of being selected for attacks. Keen (14) states that "trees from 4 or 5 inches in diameter up to those of the largest size may be attacked," and that "during endemic infestations there is a tendency for the beetles to select the weaker, less vigorous trees for attack, but no such selection is apparent during epidemic conditions." Studies undertaken by Struble (118) under endemic conditions indicated "evidence of a lack in

correlation between attacks by the mountain pine beetle and the degree of crown decadence and by Keen's and Dunning's classes among 52 currently killed trees compared during 1941." Struble states also that "there is little or no correlation between decadence type and amount of injury by insects or disease. In other words, trees whose crowns are off color or which have a distinctly decadent appearance may be free from insects or disease." He concludes that "on the basis of the information obtained thus far it is impossible to predict which trees of a given sugar pine stand are most susceptible to attacks

There is also no strong evidence of a correlation between rate of tree growth and attacks. Preliminary information from Miller's notes taken in 1924 from 25 attacked and 25 living check sugar pines revealed no relationship. Later records taken by Struble (119) in 1933, 1937 and 1941 from areas on the Sierra and Stanislaus National Forests, and totalling 83 killed and an equal number of check trees, were summed up in a report issued in 1942. In this report Struble states that "in comparing the growth rate of insect killed and living trees on - - four areas a few interesting points are noted: (1) That on the virgin areas the difference (in growth rate between insect killed and living check trees) was not great and consequently the possibility of growth rate being a factor in selection is minimized; (2) that on cutover areas the difference in rate of growth between insect killed and living check trees may be sufficiently broad as to indicate that growth rate may be a factor in selection; (3) that the growth rate of both living and insect killed trees on the cutover areas was considerably higher than the growth rates of the trees compared on the virgin areas."

Effect of beetle attack on tree.

According to Keen (14) "infested trees are recognized first by pitch tubes on the trunks of trees and red boring dust in crevices on the ground at the roots." This is true of attacks made on trees of small diameter, but probably the first outward manifestation of a beetle attack on a large sugar pine is its effect on the foliage. According to Struble (99) "dead or dying sugar pines are set off in contrast to normal green trees. The most outstanding feature is the rapid change in foliage color from pale silvery green to yellowish green, then sorrel to bright reddish brown, and finally dark reddish brown. These changes are most rapid during the summer season when from one month to six weeks elapse from the first sign to final bright reddish brown color." He states further that "trees which are gradually killed by several invasions of beetles, reflect this condition by various gradations of foliage color, from top to the bottom of the crown, while those attacked by a single invasion fade fairly equally over the entire crown," and that "the length of trunk infested by D. monticolae is subject to considerable variation, and this is manifested externally by the foliage adjoining the part of the trunk affected by the beetle."

Fading is usually observable in the summer by the time the brood has advanced to the fully grown larval and pupal stages, or after a period of 5 to 6 weeks following the initial concerted attack. According to Evenden et al (7)

"there is marked variation in the time between the initial attack and the first evidence of foliage discoloration. On some trees the foliage fades after a lapse of 3 or 4 weeks, while on others, even of the same species, there is no discoloration for several months after attack."

Effect on sap flow.

The defensive mechanism of the host tree against attacks is the resin which oozes slowly from wounded living tissue. The amount of resin which exudes varies greatly among different sugar pines attacked, and this is believed related, at least in a limited degree, to growth rate and vigor. In general, it appears that the most copious resin flows occur in fast-growing, vigorous trees, and the least in the slower growing trees growing under highly competitive circumstances.

The speed and success of attacks depends on the amount of resin exuding and the ability of the beetles to eventually overcome it. Trees growing in a fairly dense stand are quickly overcome. In Struble's (99) studies during 1933 every pole-size sugar pine tree in this type of stand on which beetles were forced to attack, through caging technique, were overcome within less than 10 days, with little evidence of resistance. In later studies during 1934 Struble (104) attempted to induce attacks on the basal trunk portion of two mature trees and found that "great resistance on the part of both trees was evident by resin flows so heavy that the bark surfaces were completely covered. Many attacks were attempted, none of which was successful, even to the point of starting an egg gallery. Dead beetles were found concentrated along the sides of each cage where they had tried to escape, but were caught in resin." These studies indicated definitely that some sugar pines are capable of surviving the attacks as long as they are able to supply the quantities of resin necessary to resist the beetles. A deficiency in resin or the eventual exhaustion of this protective substance as a result of persistent beetle attacks quickly determines the fate of the host tree.

Deterioration of the abandoned tree.

Following the death of a tree, Struble (99) states that "the foliage gradually darkens, and after a period of 2 to 3 years drops to the ground, leaving the trees standing as snags." The bark gradually drops away and within 5 to 7 years all that remains is a bleached snag. With the passing of time the snags gradually drop to the ground, some of them still standing 15 years after death.

Most of the pole-size and fast growing medium size snags fall between 5 and 10 years, and disintegrate rapidly while the older mature trees stand as snags for long periods. This apparently depends on the much greater volume of rot resistant heartwood within the bole of older trees, which disintegrates very slowly even after a snag has fallen to the ground.

BIOTIC RELATIONS

Biotic potential.

The potential increase of mountain pine beetle populations in sugar pine is enormous. For example, Struble's (99) record from 964 inches of egg gallery showed an average of 2.61 eggs per inch and an average of 150 inches of egg gallery per square foot. Hence, there was an average number of 392 eggs per square foot in the area sampled. This number is probably representative of the maximum potential per square foot of attacked bark area. The average is probably between 200 and 300 eggs per square foot.

The average number of attacking adults, based on between 7 and 8 attacks per square foot (Struble 99 and notes) is about 15 per square foot. Hence, the potential population increase per unit of bark area attacked is between 15 and 30 times the number of adults initiating attacks. The mortality of eggs and larvae is very high, as previously indicated, and the actual increase in population is only slightly above the attacking population. As indicated, the number of progeny adults amounts to between 20 and 40 per square foot, which is nearly twice the attacking population. Many of these adults die before it is possible for them to attack, and unless there is an increase in excess of this number (which is probably the case during epidemics) the population level remains fairly static.

Nutrition.

Some preliminary studies of larval nutrition were undertaken by Struble (107, 109) during 1936 and 1937 in which mountain pine beetle larvae were reared in short glass tubes containing mainly phloem of a given character or treatment. Measurements of larval development from first instar to the pupal stage were based on weight in milligrams. The most significant results of this study were: (1) outer bark failed completely to support growth and development of larvae while normal development was supported by phloem ("larvae which were fed on normal fast growing ponderosa pine and lodgepole pine phloems developed from eggs to adults in 5 weeks"); (2) larvae which fed on phloem treated by alcohol to remove sugars gained less than those which fed on phloem treated with ether to remove proteins; (3) fresh ponderosa pine and sugar pine phloem in separate tests resulted in positive correlation between moisture content and larval gain regardless of tree species or site--phloem with the highest moisture content showed greatest gains in weight per larva among fast growing phloems, but the gain was not so great on slow growing phloem even though the moisture content was also very high; (4) phloem from different heights (base, mid-hole, and top) from one sugar pine and ponderosa pine showed that "the greatest development in each case took place on basal phloem, where more moisture was present." While highly preliminary, the results served to indicate that there are differences in phloem from trees of different growth rate, and differences in phloem of different moisture content. This in turn presumably has an important bearing on the abundance of populations that can be built up within a stand.

Competition.

The number of individuals in a brood reaching maturity is limited to a certain extent by the concentration of attacks. No studies in sugar pine have been made to determine the effect of overcrowding on brood mortality, but in western white pine Bedard (31) states "it is apparent that the greatest efficiency in gallery construction is secured when there are from 9 to 15 attacks per square foot." He states further that "obviously the more bark that is destroyed (in egg gallery construction) the less food there will be for the developing larvae."

No studies have been conducted on the effect of competing insects on mountain pine beetle brood in sugar pine. There are, however, several species which may on occasions cause an appreciable reduction in brood, among which the flathead, Melanophila gentilis, the pine engraver Ips confusus, and roundheads (principally Graphisurus spp.) are most common. Infestation records of 112 sugar pines taken at different periods from 1932 to 1940 (Struble's notes) showed that 43 percent of them contained Ips top-kill infestations, 4 percent contained flatheads in the top, and 6 percent contained mixed infestations of D. monticolae and flatheads; the remaining 47 percent contained pure mountain pine beetle infestations. Because Ips confusus attacks are confined to the top, their effect as a competitor is negligible. Flathead infestations may have a decided detrimental effect, but the percentage of such infestations is low and flatheads cannot, therefore, be considered as an important competitor. Roundheads are frequently found, particularly with summer D. monticolae broods, but their effect has not been determined.

Unfavorable Weather.

High or low temperatures are known to affect the development of D. monticolae broods in sugar pine, and may even result in some mortality. In a study of development in relation to temperature at different elevations, Struble (99) found that somewhat more rapid development occurred at 7,000 feet than at 4,200 feet (in standing infested trees) even though temperatures were lower at the higher elevation. This was explained by the statement that "temperatures above 70° F. (occurring at the lower elevation) may have actually retarded development." It is doubtless probable that temperatures continuing above 90° under the bark would prove to be fatal, such as has been found to be the case in the tops of logs lying on the ground, but there have been no cases observed of broods being killed in standing trees by the effects of high temperatures.

Unseasonable low temperatures have been demonstrated by laboratory tests to cause mortality. Struble (97) found that there was 100 percent mortality of all broods at 0° F; 88 percent at 5°; 64 percent at 10°; and 28 percent at 15° F. (All of these tests were conducted on broods subjected to normal developmental temperatures for an extended period). He states that "it is apparent that the survival of D. monticolae broods when exposed to (sudden) freezing temperatures is governed by the frequency and severity of low temperatures in the locality from which the brood was taken."

In laboratory tests on summer and winter broods of *D. monticolae* larvae from sugar pine, Yuill (122) found definite regional differences in resistance to cold. He states "The larvae have a very definite seasonal cycle in their resistance to low temperatures. During the winter season they can endure much lower temperatures than in the late spring, summer and early fall." Yuill (122) continues "for example, the critical range during the summer months was 15 to +7.5° F., and in January it had dropped from +7.5 to -10° F."

For practical purposes freezing temperatures as they may occur under field conditions cannot be counted on to control this insect in sugar pine stands. According to Yuill (122) "the ability of the overwintering larvae of the mountain pine beetle to develop resistance to meet a wide range of temperature conditions explains the absence of winter mortality in this species. -- Since the overwintering larvae have the ability to develop a degree of cold hardiness sufficient to survive any winter temperatures likely to occur in the California region, winter mortality will probably never be a consideration in planning for control of this insect."

Moisture.

Information is lacking on the effect of excessive or too little moisture on *D. monticolae* broods. No studies other than the nutritional investigations discussed previously dealt with moisture relations. In those studies by Struble (107, 109) there seemed to be a direct relationship between high moisture content of phloem and larval gain. There was, however, no indication of excessive moisture or its detrimental effect on developing larvae.

All the information we have on excessive or deficient moisture is based on general observations. For example, it has been observed that poor broods have developed in logs which were sealed on the ends with paraffin to prevent drying. Excessive moisture conditions within many of the logs treated in this way seemed to be indicated. The moisture conditions were also accompanied in some cases by heavy fungus growths, which also may have caused brood mortality. Observations of broods developing in extremely slow growing sugar pines with very thin bark and phloem have indicated that deficient moisture owing to rapid desiccation was the cause of such light broods as were found there.

Light relations.

The information available on the phototropic responses of mountain pine beetle adults is rather sketchy, but sufficient to indicate that light is a profound stimulus in their flight habits. In tests with the Gordon (50) olfactometer, Hensill (56) (working with mature new adult beetles which had been removed from brood logs) found that "the beetles always moved out into the arms away from the central light and would orient themselves in the arms so as to be in the regions of least illumination. They would behave in this manner when the ends of the arms were lighted by electric lights or by weak daylight." In later (olfactory) studies with mature, naturally emerged new adults (using the same apparatus) Struble (120) noted that "the tendency of the beetles to fly because

of the light stimulus resulted in many of them getting turned over on their backs. The apparent confusion resulting therefrom indicated that the light factor was responsible for much erratic behavior and loss in the time of running tests." ^{1/} Under natural field conditions the flight of adult beetles occurs only during daylight hours, and the light factor may be presumed to be the principal flight stimulus, and doubtless the most important factor enabling them to reach their host.

Enemies.

Parasitic and predacious insect enemies of the mountain pine beetle in sugar pine have been reported from time to time by different men working with this insect. In 1918 Miller (65) stated "during investigations conducted in the Yosemite National Park, California, and in the vicinity of Ashland, Oregon, pertaining to the damage and control of the mountain pine beetle, it was found that this bark beetle was host to at least two species of Hymenopterous parasites; one species of Dipterous parasites; three species of Coleopterous predators and several species of woodpeckers. Owing to the limited amount of data obtained, the percentage of control involved by these natural enemies was not ascertained." Person (85) states "on February 20, 1928, A. Wagner collected a number of predacious and other insects from beneath the bark of a D. monticolae infested sugar pine found near Northfork. This material was looked over by the writer and 3 Temnochila virescens larvae, 6 Thanasimus nigriventris larvae, 2 Deretaphrus oregonensis adults and 1 Tenebroides sp. adult were saved." In a study of parasites Person (89) stated "another species determined by Rohwer as belonging to this genus (Hoptrocerus) is apparently an internal parasite. It was observed by J. E. Patterson '(unpublished)' while ovipositing in a Dendroctonus monticolae Hopk. larva, exposed when the bark was stripped from an infested sugar pine." Person stated also that the dipterous larva Medetera aldrichii (Wh.) "is probably of most importance as a parasite of D. monticolae." Struble (99) states "the destruction of mountain pine beetle broods is accomplished in nature by various predacious and parasitic insect enemies and birds, but because of the physical handicap encountered by most of them of extremely thick bark the amount of control is minimized. The larvae of (Rhoclerus sphegeus Lec.) are common under bark of any thickness. Temnochila virescens, Aulonium longum, and Flatysoma punctigerum are commonly found under the bark as well as many other predacious Coleoptera of lesser importance, but the extent of control they exert on D. monticolae broods is indefinite." In this same report Struble states also that "certain parasitic Hymenoptera are common in infested areas of thin bark, of which Coeloides sp. is most important. Parasitism of broods by this insect in bark less than $\frac{1}{2}$ inch thick is very high, but the occurrence of D. monticolae broods in thin bark is infrequent in sugar pine."

^{1/} The use of immature beetles in Hensill's tests is believed responsible for the negatively phototropic responses as opposed to Struble's results with fully mature and naturally emerged adults. Hensill's results cannot, therefore, be considered a normal mature adult response to the light stimulus.

In lodgepole pine, DeLeon (37) noted that "of all the insects associated with D. monticolae those that belong to the genus Coeloides are perhaps of greater importance in biological control of the beetle than any of the other investigated species." Speaking of predators, parasites and associated insects in lodgepole pine, DeLeon (39) states that "in the case of the mountain pine beetle the progeny emerging from a tree would be at least two to three times as numerous as its parents that killed the tree were it not for the insects which destroy the immature forms of these beetles."

In western white pine also, DeLeon (40) observes that "Coeloides sp. was found to be the most important parasite of D. monticolae. However, the distribution of the larvae of this parasite in infested white pine trees is not as even as in the lodgepole." Among the predacious insects DeLeon (40) found that "the larvae of this insect (Medetera aldrichii Wh.) are the most valuable predators of the mountain pine beetle in both lodgepole pine and western white pine, but no method has yet been devised to enable one to determine how valuable they are. It is probable, however that they destroy much more brood of the beetle than is destroyed by Coeloides, as the eggs of the fly are laid in trees as soon as they are attacked."

It may be impossible to determine the exact amount of control by insect enemies. DeLeon (40) states that "on the average it is probable that not over 40 to 50 percent of all the brood of the mountain pine beetle is destroyed (by Medetera aldrichii), although no figures are available for this supposition. In spite of the high destruction to the brood it is doubtful if this insect is as valuable a factor in controlling the brood of the beetle as is Coeloides, whose average parasitism is about 16 percent." Bedard, (30) states "these insects (Coeloides dendroctoni Cush. and Medetera aldrichii Wh.) are so valuable as controlling agents that sometimes from 80 to 98 percent of the mountain pine beetle within certain infested trees is destroyed by them." In later work DeLeon (3) concluded that "Coeloides dendroctoni Cush. is the most important parasite of this scolytid in western white pine and lodgepole pine in these regions (Washington, Idaho, Montana), and parasitism frequently runs as high as 80 or 90 percent. -- Average parasitism ranged from 4 to 23 percent, depending on the age of the infestations, but in individual trees it frequently reached 90 percent." Regarding predators DeLeon (4) concludes "Medetera aldrichii Wh. is the most important predator of the mountain pine beetle infesting lodgepole and western white pine. It probably destroys 40 to 50 percent of the brood of this beetle."

Birds account for a considerable portion of the mountain pine beetle in the larval, pupal and adult stages. Most of them are woodpeckers, and they are most active during the winter and spring months, flicking away the outer bark, particularly in the upper part of the infested trunks, to obtain the broods within the inner bark. According to Struble (116) "the most important species in the control of sugar pine infestations are the hairy woodpecker, western piliated woodpecker, the white headed woodpecker, and the Lewis woodpecker."

In the northern Rocky Mountain region, Rust (93) analyzed the gullet contents of nighthawks and woodpeckers and found considerable numbers of D. monticolae adults. Among the woodpeckers he found the Alpine 3-toed and Rocky Mountain

woodpeckers to be most important. He stated that "the woodpeckers being much more abundant than the nighthawks -- (they) are undoubtedly the most beneficial birds in the region."

Little is known concerning diseases of the mountain pine beetle or their possible effect on beetle populations. Diseases have been suspected as the cause of high mortality in certain trees many times, but no studies have been initiated to determine the nature or identity of the possible causative organisms. According to Struble (116) "Examples of natural control that can be attributed to fungi and bacteria are found almost every year in the brood failures in certain trees that had been heavily attacked by the mountain pine beetle." In these failures there are often no indications of brood beyond the completed egg galleries, but frequently there are "black and decaying first and second stage larvae," killed apparently by some microscopic organism.

Associated Insects.

No studies have been undertaken yet to evaluate the full role of associated insects. Hence, the information known is primarily the result of a number of stem infestation records and observations which were not reported on.

The competitive effect of the more common associated insects such as Ips confusus, flatheads, and roundheads was considered previously. Among these insect species, the effect of roundheads was not determined in the sugar pine association. However, in a discussion of associated insects in western white pine, DeLeon (40) found that "the larvae of (Acanthocinus obliquus Lec.) -- in feeding consume practically everything in their path, and thus where numerous, are often directly destructive to the brood of the mountain pine beetle. It is also probable that they destroy some larvae indirectly by lessening the food supply."

Besides being competitive these insects also are believed to aid the mountain pine beetle frequently in overcoming the resistance of a tree. For example, the attacks in the top and branches of sugar pine by Ips confusus often precede successful mountain pine beetle attacks. The same may be said of flatheads, and to a lesser extent of round heads, Pityophthorus sp. and D. valens, all of which attack living bark and phloem tissue. Leaf and stem-feeding scale insects are probably least important as sugar pine weakening agencies, which render trees susceptible to bark beetle attacks.

There are a number of associated insects in addition to the species mentioned which have nothing to do with weakening the host tree. The insects in this category are dependent on the death of a tree, and are attracted soon after the resistance of the host has been overcome. Some are predacious, others are parasitic, and many are presumed to feed on dead or decaying tissue or fungi. Except for a few of the more important predators and parasites, no studies on the habits or life cycle of the large number of species have been undertaken in sugar pine.

In western white pine the associated insect fauna is quite similar to that in sugar pine. Studies by DeLeon (41) in western white pine resulted in a listing of many of the more important species. A few of those which were

stated to be definitely predacious on the mountain pine beetle are as follows:
"COLEOPTERA: Staphylinidae, Nudobius sp., Quedius longipennis Mann., Quedius sp.; Histeridae, Isolomalus manicus Gey., Platysoma punctigerum Lec., Plegaderus sp.; Cleridae, Enoclerus lecontei (Walc), Enoclerus sphegeus (Fabr.), Thanasi-
mus dubius Fabr.; Ostomatidae, Temnochila virescens (Fabr.); Cucujidae, Cucujus
clavipes Fabr.; DIPTERA: Xylophagidae, Xylophagus abdominalis Loew.; Dolicho-
podidae, Medeterus aldrichi Wh."

Dissemination.

The spread of mountain pine beetle infestations from one tree to another close by or at some distance occurs as a result of the adult flight habits following maturity and emergence from the parent host tree. No specific studies have been undertaken on dispersal, the factors influencing directional behavior during flight, the factors involved in the selection of a host tree, and the distance travelled by the adult mountain pine beetle in the sugar pine association.

Some records of flight in the lodgepole pine and western white pine association in the northern Rocky Mountain areas indicate the beetles may fly for considerable distances. Evenden et al (7) state "records show that infestations of the mountain pine beetle have crossed timberless areas from 15 to 20 miles in width. This fact indicates that these beetles are able to make long flights or can be carried by air currents, with perhaps both factors playing an important part in such dissemination. Although such flights occur, there is no conclusive evidence as to the distance or direction these insects will move. The local spread of an infestation is no doubt governed by the availability of host material."

Preliminary studies by Terrell (121) with wind-vane traps, indicated the possible influence of air currents in dispersal. He states that the traps "were always faced into the wind by the action of a weather-vane tail; therefore, collections were made only of insects being born with the wind." He found that "20 of the 65 species of Coleoptera collected were bark beetles. The mountain pine beetle was taken from the traps on both Roundtop and Sullivan mountains. Although these traps were not far from timber, insects passing this point could, no doubt, have been blown for many miles before descending to the ground." Further tests by Terrell to determine the height of flight of the mountain pine beetle by an airplane trap and weather bureau kite indicated that scolytids fly at lower elevations. No D. monticolae adults were taken.

Tropisms.

Few studies have been undertaken to determine the response of the mountain pine beetle to various stimuli considered important in directing the beetle to the host tree. It is a matter of common knowledge that the beetle is readily attracted to trap logs, windfalls, lightning-struck trees, slash, etc. as well as to living trees having no apparent injury. The complexity of factors involved in directing the beetle from the place where it was reared to a new location for its attacks and broods is still little understood.

The initial investigative work consisted of various attraction studies with this beetle in lodgepole pine. Patterson (75) found that "successful attacks by the mountain pine beetle may be induced on lodgepole pine trees by caging infested material around the base of the tree, by leaning infested sections of logs against the base of trees, and by transferring live beetles from attacked trees to green trees." In further studies by Patterson (77), attempts were made to induce attacks in lodgepole pine. "Trees were felled in the open forest; the bark on the basal portion of others was scorched with blow torches; and still others were artificially defoliated by plucking or snipping off the needles and by burning the needles. Other means were also employed, such as transferring living and dead beetles and fresh pitch tubes from attacked trees to green trees. Nailing infested sections of attacked trees to green trees and making nail holes through the bark of living trees." Studies by Struble (118) on the possibility of a relationship between crown decadence of sugar pine and attacks by the mountain pine beetle were discussed earlier.

These studies served to show quite conclusively that the mountain pine beetle could be attracted to host material, but that among living trees it was impossible to predict which one would be selected on the basis of visual tree characters. As a consequence it became necessary to consider the analysis of some of the most obvious factors believed to be involved in attraction. Light, temperature, odor, and air currents were considered as primary. The light factor which is believed to induce flight was discussed earlier.

Temperature is extremely important in stimulating the movement of the adult, and observations in sugar pine generally indicate that the emergence of new adults from infested trees is stimulated by temperature alone which must be 60° F. or above in the sugar pine type before appreciable emergence takes place. Temperatures ranging between 70° F. and 85° F. appear to be optimum for both the activity and development of this insect.

The factor of odor may be of greatest importance in directing the beetle to its host. It was on this assumption that studies were undertaken by Struble (120) in sugar pine. The Gordon (50) olfactometer was used in tests of the attractiveness of phloem from trees varying in vigor or decadence, newly attacked trees, lightning-struck trees, different heights of trees, sapwood, foliage, etc. In this apparatus it was possible to control light, temperature, odors, and air movement. The fact that "most of the tree materials tested repelled the beetles regardless of their possible attractiveness to beetles in flight" indicated the need for greater refinement in technique and considerably more research work before conclusions were possible.

Host Selection.

The host selection principle, an hypothesis advanced by A. D. Hopkins, presumed that if D. monticolae was reared for successive generations on the same host, it would continue to prefer to rear its broods in that host. This principle was tested by Keen (60) in 1916 who concluded that "sugar pine is the preferred tree regardless of what tree the beetles originated in." He stated "that given an equal chance, beetles even from yellow pine exhibit a preference for sugar pine." Keen comments that "it may be that

in this locality (southern Oregon) sugar pine is the preferred tree because the beetles have fed on it for generations and that they simply attack yellow pine by chance or when thrown in contact with it."

Evenden (44) presented evidence from field observations on a number of insect control projects which indicated that the mountain pine beetle prefers to breed in a single host as long as that host is available, but will breed in other host trees when there is a scarcity of the preferred host.^{1/} Bedard (29) stated "it would seem that there is a decided preference shown by the mountain pine beetle in its selection of a host, white pine being preferred, when the beetles emerge from white pine; with Engelmann spruce, lodgepole pine and white bark pine preferred in the order named." He pointed to the necessity of considerably more studies before conclusions were possible.

Further studies of host selection by Struble (105) in sugar pine resulted in the observation that "under natural conditions there appears to be a selectivity for one species over another which may be dependent on inherent qualities developed through continuous breeding in a specific host. Strong evidence of this is found in mixed sugar pine-ponderosa pine stands of California where sugar pine is decidedly preferred even though ponderosa pine is the predominant species." Struble states, however, that "cage control experiments -- using freshly cut green logs from a number of hosts failed to show any decided selection between four species of pines tested; sugar pine, lodgepole pine, ponderosa pine, and Jeffrey pine."

Epidemiology.

Fluctuations in the intensity of mountain pine beetle infestations in sugar pine stands occur at indefinite intervals. There are apparently no well defined cycles of activity. Infestations of unusual intensity often appear suddenly, causing considerable damage, and subside as quickly as they appeared. At other times there is a gradual rise from low to high to low again covering several years.

The infrequent periods and rather indefinite character of fluctuating infestations have offered only a limited opportunity for studies to be made on the causes underlying them. What few studies that have been made indicate there are 3 general types: (1) the endemic or normal infestation which is generally low and prevalent for long periods; (2) the sporadic infestation or localized sudden flareup in which a large number of trees within a localized area are killed; (3) the epidemic in which broad general areas are infested and great numbers of trees are killed during its course which may last for several seasons.

The character of trees attacked differ considerably from those attacked by the western pine beetle. Keen (14) has indicated the tendency of the western pine beetle to select decadent, weakened trees under endemic conditions, but the

^{1/} Occasionally freak attacks are made on trees not normally a host of this beetle. For example, in 1932 Miller noted an 8-inch white fir which contained several D. monticolae attacks along the bole. Also, Struble (105) reported freak attacks on incense cedar, but all adults had died.

lack of such selection during epidemics. Struble (118) indicated there is no apparent choice exhibited in selection between vigorous or decadent sugar pines attacked by the mountain pine beetle, and because of this the beetle may be more aggressive than the western pine beetle. However, Struble (99) states "From the data obtained by caging trees of varied rates of growth, it was found that with a given number of beetles per square foot of area attacked, it was much easier for them to become established in slow growing trees than in either moderate or rapid growing trees. All slow growing trees were overcome and completely killed within a short period, while varying degrees of resistance was shown in the medium and fast growing groups."

One of the causes for a sudden upward trend from normal endemic infestations can be attributed to windfalls. In a study of 2 outstanding windfall areas in California (Upper Lake Windfall, California National Forest, 1921; Inyo-Mono Windfall of 1923) Miller (17) states "in both situations studied, bark beetle epidemics appeared with such suddenness in standing timber about the windfalls that their origin must have been largely the beetles coming from the windthrown logs. These epidemics subsided with equal suddenness after reaching their peak in the standing trees. - - The period between the occurrence of the windfall and the bark beetle outbreak in standing timber ranged from 2 to 4 seasons."

More recently Struble (110), in speaking of a localized outbreak of the mountain pine beetle in a cutover reserve sugar pine area of the Sierra National Forest, states that "During the winter of 1935-1936 a large number of trees was blown down by the wind, particularly in the vicinity of Signal Peak and southwest of Iron Mountain. The current infestation is centered in the windfall areas. The concentration of the mountain pine beetle in a large number of smaller trees (within the windfall areas) suggested strongly the windfall origin of the 1936 infestation."

Another cause of sporadic increases in infestation is attributed to slash areas. This has been found to be true, particularly in areas where heavy slashings, consisting of large numbers of "long butts," cull logs, and tops have been left in the woods. The most outstanding example was recorded by Patterson (79) from Big Creek Basin in the Stanislaus National Forest from 1931 to 1933. The slash area covered 640 acres and affected surrounding virgin timber, predominantly sugar pine, in an area comprising 5 sections. The losses to standing sugar pine timber as a direct result of slash breeding of *D. monticolae* during the 3-year period amounted to 828 trees having a volume of 3,997,670 board feet. As a result of an intensive study of this area, Patterson concluded:

"Cull logs, butt cants, and broken sections of trunks of sugar pine are especially attractive to the mountain pine beetle and that slash of this character is favorable breeding material for these beetles."

"Mortality is relatively low in broods developing in slash that is well protected from the sun by dense brush cover and thick understorey such as was prevalent on this area."

"That a flare-up in infestation in standing timber may be expected when logging operations are suddenly stopped. That such increased infestation

occur in the immediate vicinity of the slash; and that there is an actual reduction in losses in more remote areas.

"That it is hazardous to leave entire trees, or any other large amount of breeding material as was done in this operation; since broods breeding in such material develop normal progeny and greatly increase the beetle population.

"The greatly increased epidemic infestation was of short duration in this case and it followed the same cycle as other slash infestations previously studied. On this area the epidemic subsided within 2 years."

One outstanding character of these localized sporadic infestations is their suddenness both as to starting and in ending. This is due apparently to the ability of beetles to build up large populations in the prostrate non-resistant logs. The beetles emerging from such infestations attack in great numbers the standing trees, causing severe losses, but owing evidently to stand resistance the pressure of populations is soon lowered again to an endemic level.

Widespread general epidemics of the mountain pine beetle in sugar pine since studies of this problem were instituted have been too few to give us a basis for determining the causes. According to Miller et al (68) in 1944 "records of the insect control projects undertaken on the Sierra National Forest show that within the past 30 years, there have been 3 major periods when the mountain pine beetle was aggressive generally. The peaks appear to have been in 1917, 1924 and 1932." In speaking of the 1932 epidemic Struble (99) stated that there was "widespread damage to magnificent timber of outstanding commercial and aesthetic value in the central Sierra region, embracing the Stanislaus and Sierra National Forests, and Yosemite, General Grant and Sequoia National Parks."

A few theories have been advanced as to the causes of general epidemics and have been loosely termed by Miller et al (68): "(1) the climatic theory; (2) the light burning theory; and (3) the biological cycle." According to the climatic theory "there has long been a general belief among those interested in this problem that beetle outbreaks are directly related to drought periods." The light burning theory presupposes that moisture is removed from the ground by reproduction and thus weakens stand resistance; the removal of reproduction by light burning on the other hand, would improve resistance and prevent epidemics. The biological cycle presupposes that "bark beetle populations fluctuate with a certain degree of cyclic rhythm or periodicity due to the operation of biological factors." Thus the effects of temperature, predacious insects, birds, associated insects, slash, wind-falls, etc. may figure in one way or another in their effect separately or in combination to influence the pressure of bark beetle populations.

ECOLOGICAL RELATIONS

There are many factors which in one way or another affect the reproduction, growth, and survival of sugar pine. The action independently of single factors, the combination of 2 or more factors, or the interaction of all

factors in influencing the condition of this host is known only in a general way. Their influence upon the attacks by insects, particularly by the mountain pine beetle, is still largely in the realm of speculation.

Some of the general requirements of sugar pine are indicated by the distribution and growth of this tree species. According to Betts (1) "The range of sugar pine extends from the Coast and Cascade Ranges and Sierra Nevada mountain ranges of southern Oregon along the Coast Ranges and Sierra Nevada of California through southern California in scattered stands and into Lower California in Mexico. The largest trees and heaviest stands are found in California from Tulare to Eldorado Counties in cool, moist sites on the west slope of the Sierra Nevada at elevations of from 4,000 to 7,000 feet. Sugar pine frequently occurs in pure stands of about an acre but is seldom, if ever, found on larger areas without other species in mixture, principally ponderosa pine, California incense cedar, white fir and Douglas-fir. Sugar pine attains an age of about 500 years and grows to a larger size than any of its associates except the sequoias with which it is occasionally found. -- One of the most remarkable characteristics of the tree is its ability to sustain its rate of growth up to a very advanced age. -- Considerable moisture in both soil and air is essential for the rapid development of sugar pine throughout all stages of its life, particularly during the seedling and sapling periods. The tree demands a large amount of light except in early youth."

Phenological Relations.

Climate probably exercises a greater influence on the general distribution and health of sugar pine stands than any other single factor. Climatic factors alone are believed to be responsible for the restricted zones in which this species has become a dominant component of the mixed conifer type in which it occurs. Its restricted distribution to the elevation levels between 4,000 and 7,000 feet in its optimum zone of development in the central Sierra pine belt is probably due primarily to the optimum climatic conditions found on these areas. Its occurrence at lower elevations in the northerly latitudes and at higher elevations in the southerly latitudes of its range is believed due to the similarity of climates. The scattered character and poor development of trees in the outer fringes of the sugar pine belt are indicative of a struggle with climatic factors.

Silvicultural and environmental relations.

1. Site factors. Within the climatic zones favorable to the development of sugar pine there are other factors which doubtless exercise a localized influence on the distribution and health of this tree species. The topographic character of the landscape, and the composition, character, and depth of soil are doubtless among the more important physical factors which may limit the development or survival of this tree and determine the site quality. Within the optimum development zone the poorest sites are found as a rule on steep ridges broken by deep ravines, or on slopes which are deficient in good soil. These conditions combined with direct exposure to the sun on south and west slopes are the least conducive to good development. The best sites are those containing deep, well drained soil which is rich in humus, on level or rolling terrain, and on north slopes. Within the

optimum zone the highest percentage of sugar pine stands are site II quality. Sites I and III are common, while site IV is rare.

The volume per acre of sugar pine varies from 10,000 board feet per acre (approximately) on the poorest quality sites to over 50,000 board feet per acre on the best quality sites, with an average of approximately 25,000 to 30,000 board feet per acre within the mixed conifer forests in which it is a dominant component. The greatest volumes are found in the type composed mainly of sugar pine and white fir on the best sites.

Few studies have been made to determine whether there is a relationship between site quality and mountain pine beetle hazard. What data there are indicate the lack of any relationship, but rather that there are other factors which apparently exert a greater influence on the beetle hazard. The factors of competition and overmaturity of the stand, for example, appear to be more important and in this respect there is indicated that some of the greatest hazards are on the better sites.

2. Environmental factors.

Slash areas resulting from logging operations, power line clearings, highway right-of-way clearings, etc. affect the residual sugar pine stand in different ways. While few specific studies have been made in connection with any particular type of slash area, numerous observations on slash areas have indicated the development of conditions favoring increased mountain pine beetle activity. (One outstanding example in the Big Creek Basin (Stanislaus) was discussed previously.) The opening of the stand on logged areas has often resulted in broken tops and windfalls, which in addition to logging slash has resulted in a rapid increase in beetle populations and subsequent killing of sound trees of the residual stand. Slash resulting from power line and highway clearings has been found to contribute directly to increased infestations in sound timber nearby, as a result of breeding and subsequent increases in beetle populations in the heavy slash.

The opening up of virgin timbered areas to full sunlight and subsequently to increased temperatures and lessened humidity may in some instances be detrimental. The drying out of soil, the disturbance of ground cover, and often the root systems, may be the cause of some weakening. Injuries to the crown or main bole sustained by logging have been observed frequently to result in poor appearing, apparently weakened trees which presumably are susceptible to mountain pine beetle attacks.

The importance of windfalls in virgin pine areas as a source of beetle infestations was discussed previously. Aside from this menace the occurrence of windfalls opens up the timber and may improve growing conditions for the residual stand by lessening competition for food supply and moisture. Frequently, however, there is mechanical injury to nearby timber, such as broken limbs, damaged boles, etc. caused by the falling trees.

The destruction and damage caused by fire in virgin stands of timber is well known. In the sugar pine type there are no exceptions in the number of trees killed outright and of those injured in one way or another, or of the damage to soil, ground cover, and reproduction. The general weakened conditions of surviving sugar pines renders them particularly susceptible to mountain pine beetle attacks. Generally, infestations have been observed to develop within 1 to 2 years after the burn and persist for 2 to 3 years.

Infested fire injured sugar pines are not generally considered a serious menace to uninjured virgin timber. However, there have been instances when populations built up in these areas have done considerable damage. One recent case was reported by Struble in a memorandum concerning an infestation in Yosemite National Park in 1943. He stated that activity was "centered in the vicinity of the burn lying to the south of Big Meadows. The burn occurred in October 1941. In the burned area and in areas adjacent to the burn, hundreds of recently faded trees were observed." This infestation died out rather suddenly following the kill of fire injured trees and the institution of direct control by the National Park Service.

The effect of mountain pine beetle infestations upon a stand of timber, aside from the menace to living trees, is to open up the stand. In this respect the effect is similar to conditions caused by windfalls. The effect is variable, and what few studies have been made indicate that: (1) there were improvements in the residual stand in some cases by decreasing the competition for soil moisture, etc.; (2) that the opening of the stand apparently stimulated dense growths of white fir reproduction in most instances and thus a situation of greatly increased competition was created which appeared to be more detrimental to the residual virgin stand than the original situation before the appearance of the beetle. As a typical example, a one-acre plot (SP-2) which was established in 1943 by Struble showed definitely that the residual sugar pine stand was well along the way toward dying out, and was being replaced by a dense thicket of fir reproduction. On this plot originally there were 44 mature sugar pines having a volume of 78,150 board feet. Within 15 years prior to 1943, 17 of these trees with a volume of 29,000 board feet had been killed by the mountain pine beetle.

Tree Condition.

The health or vigor of the individual tree has been presumed to have much to do with relative susceptibility to insect attacks. What few studies that have been instituted in this regard, however, have yielded little in the way of proof that there is a relationship. It was indicated by Struble (118, 119) earlier that the degree of decadence or vigor in the crown of a tree and also the rate of growth were not found to correlate with mountain pine beetle attacks. Thus, it would appear that whatever weaknesses are indicated by the general appearance of the crown are independent of any effect that they may have in influencing beetle attacks.

The vigorous or decadent appearance of a sugar pine as indicated by the shape and fullness of the crown is in general correlated with the width of annual rings and the age of the tree. Young trees growing in an open stand free from excessive competition grow most rapidly; those growing in heavy stands under highly competitive conditions grow more slowly. The growth rate

of older trees also is influenced by competitive circumstances; the slowest growing, most decadent trees are usually the oldest ones growing under highly competitive circumstances. This has been observed to be true on any given site, with variations in age, growth rate, and height influenced by the growing site.

There are a number of agencies which tend to weaken trees, in addition to the influences of site or climatic conditions. The effect of lightning in a very high percentage of the cases is such that insects attack and kill these trees within a few months after injury. Drought is slower in its effect, but is considered to be an important tree weakening agency. The effects of fire scars are often serious, admitting the entrance of rots, and often badly injured trees are blown over by the wind. Top-killed trees, resulting from aggressive Ips, flathead, or Pityophthorus attacks are definitely weakened, and often become the victims of mountain pine beetle attacks.

The effects of fungi and mistletoe are lesser known. The common oak root fungus, Armillaria mellea, has been found as an aggressive killer of young sapling and pole-size sugar pines in different parts of its range. Studies by Struble (118) indicated that the branch injury (die back) on mature sugar pines might be caused by a fungus or virus infection. The blue-stain fungus associated with insect attacks probably hastens the death of a tree or the part of a tree affected by insects, but its aggressiveness is apparently dependent on previous injury by insects or some other factor.

Mistletoe is in many cases very prevalent and frequently it causes badly deformed crowns through the growth of witches brooms. Mistletoe is apparently most frequent on poor sites, and trees heavily affected by it have been found to be highly susceptible to attacks by the mountain pine beetle. According to Struble (118) "there is little doubt but that this parasitic plant (mistletoe) is a distinct weakening agency, not only on mature timber, but also among trees of all ages from seedlings to mature trees." According to W. W. Wagener in correspondence dated September 11, 1941: "The sugar pine mistletoe, Arceuthobium campylopodum blumeri, ordinarily causes greater deformation and leads to killing of affected parts sooner than the form on ponderosa pine."

There are several insect species which have been found to feed on the foliage and twigs, among which scales are most prevalent. According to Struble (118) in a study of the causes of crown decadence near Green's Mill, Sierra National Forest, "The pine leaf scale Chionaspis pinifoliae (Fitch) was found to be the most consistently distributed, but general damage to foliage was not detected on any of the trees in which it occurred. The most evident damage to foliage was in the form of yellowish or etiolated spots, the cause of which was suspected to be associated with leaf-hoppers. Although they were never seen actually feeding on the foliage, the presence of numerous leaf-hoppers seemed to indicate that they may in some way be linked with damage. Two species were identified by F. W. Oman as Aceratagallia lyrata (Bak) and A. californica under Hopk. U. S. 23751."

Among sapling and pole-sized stands of sugar pine growing under highly competitive conditions, the scale insect Matsucoccus paucicatrices has been found to cause deformation and killing. In studies of this problem,

McKenzie (16) states "On the basis of observations made in the field, Matsucoccus paucicicatricis apparently has a definite weakening effect on younger trees from sapling to pole size. Some trees have been killed outright as a result of the scale feeding, but the more common type of injury observed is the deformation of young trees due to the killing of terminal leaders and lateral branches. Infestations of this scale appear to be favored by conditions of highly competitive growth, although injury caused by this insect has been observed on sugar pine reproduction rather amply spaced. A canopy-like situation produced by larger trees overhead seems to be extremely favorable for developing scale insects, and flagging injury appears to be more prevalent under these growing conditions. Sugar pine trees growing on rather poor sites have also been found highly susceptible to scale insect attack and branch flagging."

DIRECT CONTROL METHODS

The control of the mountain pine beetle in sugar pine stands has been so closely linked with western pine beetle control in ponderosa pine that there has been little separation, either in the detection of infested trees or in methods of eradicating the beetles. The principal reason is that the two species of trees are so closely associated in mixed stands. Also the tremendous losses caused by the western pine beetle in ponderosa pine have tended to overshadow the importance of other bark beetles in pine stands, and the control of those pests has always been included as a part of the general beetle control program.

The mountain pine beetle frequently occurs as the only aggressive insect in these mixed stands, attacking principally sugar pine, and also ponderosa pine. In such instances the control policy usually followed has been determined largely by the management status of specific areas in which the infestation occurs. In park or other highly used recreational areas where sugar pines are the main asset, control work is recommended regardless of the size of the infestation. On commercial forests control work is recommended whenever the number of infested trees rises above what is considered a normal endemic loss. In most virgin sugar pine areas, the loss of 10 trees or more per section is serious enough to justify immediate action, primarily because of the great volumes involved. According to Evenden et al (7) "In determining the seriousness of each specific situation, thought must be given to the possible development of epidemics that may subsequently spread into adjacent uninfested forested areas. Abnormal supplies of attractive host material, of which windthrows are of greatest importance, are potential sources of destructive mountain pine beetle outbreaks. Such accumulations must receive the necessary attention to prevent the development of the abnormally large broods which occur in such material."

Surveys.

The reporting of initial bark beetle outbreaks and the surveys that must follow are discussed in detail by Keen (12, 14, 62) and to a lesser extent by others (Johnson, 59; Buckhorn, 35) long associated with control projects. Much of the summarization of detail contained within the reports and

publications on surveys has been included in a summary of the western pine beetle by Miller (69), and hence only the more important highlights will be included here which are pertinent to the control of the mountain pine beetle.

According to Keen (14) "The first reporting of outbreaks devolves upon the timber owners, the State or Federal forest rangers, or others who are primarily responsible for the protection of forests. Such work is analogous to that of the forest-fire detection system. One of the first things to be done is to determine the trend of the infestation -- whether normal, increasing or decreasing -- and the possibility that natural control factors may soon become operative. -- The next step is to make an extensive survey of the area to determine what parts must be included in the control program, the number of trees that will require treatment, and the probable cost of the work."

The method to be employed in making these surveys is dependent on the topographic features of the infested area. Keen (14) states: "The topographic method, or red-top survey, is particularly well adapted to estimating bark beetle losses over large forested areas of rough topography, where a large part of the forest can be viewed from open valley, ridges, or lookout points.

-- The sample-strip method is adapted to estimating bark beetle losses on flat or gently rolling areas where viewing from a distance is impossible. -- Ordinarily a 5 percent sample of an area should give a reasonably good estimate for control purposes, and on large areas a 1 percent sample is often sufficient."

In using the topographic viewing method the estimator (Keen, 62) "equipped with binoculars and a topographic map of the area 'gridirons' the country by travelling along the ridges or open valleys or wherever an unobstructed view may be had of most of the timbered area. At selected points along the route, the opposite slopes or areas visible and not more than 2 miles away are viewed either with the naked eye or with the binoculars, and the red, sorrel or faded trees counted. These are spotted on the map within the area which has been viewed."

In using the sample strip method (Keen, 62) "the observer travels through the forest along some routes of known position and length, such as a forest road or trail, but preferably along a section line or compass line, so as to obtain an impartial cross section of the area uninfluenced by the special types of trees which might be encountered along ridges or canyon bottoms. Distances are determined by pacing, or using the known distances between fixed points, such as section corners or topographic features located on accurate maps. Without attempting to blaze or mark the trees, the numbers of fading, sorrel, or red-top trees are counted within a specified distance on either side of the line of travel."

Spotting.

The intensive or spotting survey is inaugurated soon after the machinery has been set up for a regular direct control project. This survey is accomplished by one or more crews of men trained in the detection, location, and recording of infested trees over all terrain included in the project. A 3-man crew is most desirable where the country is strip-cruised. According to

Keen (62): "one man acts as compassman, carries the line and does the mapping, while the other two men do the spotting and work within the strip on either side of the compass line."

The spotter is responsible primarily for the detection of infested trees. Johnson (59) states "these (trees) are noted by certain external indications of infestation; namely, fading or faded foliage, fresh or recent pitch-tubes on the bole of the tree, sawdust (frass) in bark crevices and on ground at the base of the tree, woodpecker work, either scaling or individual holes, in the bark of the bole, and exudations of pitch which form long stringy accumulations on the bark of the bole of Jeffrey, sugar and lodgepole pines."

The spotting of infested mature sugar pines is often complicated by the character of attacks made on them by the beetle. This was indicated by Struble (99) who stated: "It frequently takes 3 or 4 separate attacks - - to complete the death of many of the largest trees. Pole-size trees and those with diameters less than 40 inches d.b.h. are often killed by a single invasion over the entire length of trunk." According to Patterson (84): "Frequently the killing of one of these great trees is a process that lasts for an entire season or longer. The attack may occur in the upper 25 or 30 feet of the bole, and an entire generation of beetles will develop in this part of the tree before a second or third attack has been made, when the infestation reaches the base."

The question usually raised in the spotting and marking of top infested trees is whether or not they will survive or will be killed by successive beetle attacks. No set rule has been adopted and usually the decision is left up to the discretion of the spotter. The "rule of thumb" that has been used on certain projects with some degree of success is to mark for treatment all trees with top fades which include one-third or more of the total crown. If trees with fades less than one-third of the total crown fail to recover, they may be left for later treatment.

Mechanical Control.

Some of the methods to be adopted in the control of bark beetles were recommended by Hopkins (11) in 1910. They were: "(1) Utilize the infested timber and burn the slabs during the period in which the broods of the destructive beetles are in the immature stages or before the developed broods emerge from the bark; or (2) fell the infested trees and remove the bark from the main trunk and burn the bark if necessary; or (3) remove the infested bark from the standing timber and burn the bark when necessary; or (4) immerse the unbarked logs in ponds, lakes, or streams where the bark will remain soaked long enough to kill the insects; or (5) remove the unbarked logs or products to a locality where there are no trees liable to attack within a radius of 20 miles or more."

1. The fell-peel-burn method. With the exception of the fell-peel-burn method, most of the others mentioned by Hopkins have been little used in large scale control of sugar pine infestations primarily because of cost, and inaccessibility of infested trees in relation to sawmills. Most of the projects involving infested sugar pine have been located in the rough, and often inaccessible terrain of the central and southern Sierras. The large

size of trees and the scattered character of infestations also have been stumbling blocks to control by logging or methods other than by burning.

The fell-peel-burn method is discussed by Keen (62). He states: "Whenever possible the trees should be felled in an open place, where their treatment will cause the least possible damage to reproduction and green timber. - - On sloping ground the trees should be felled downhill or uphill and never on the contour, as otherwise fire will be hard to control. 'Bedding' heavy logs, i.e., keeping them off the ground is sometimes desirable where burning conditions are unfavorable. - - All infested bark on the top half of the log to well down on the sides should be removed and stacked along the log. The peeling should continue far enough into the tops so that the burning of the tops, brush and limbs will destroy the beetles in the remainder of the trunk. - - Infested bark on the stumps should be peeled and piled along the log to burn. - - The fire should be large enough to burn completely all the infested bark and yet not so large as to make it difficult to control or to cause damage to adjacent standing timber. - - A fire line should be constructed just as soon as there is any tendency for a fire to remain active overnight. It should be constructed as close to the tree as is compatible with safety in burning. The line itself should be a cleared path at least 2 feet wide, raked or shoveled down to mineral soil, and should completely encircle the tree but exclude the stump. This precaution is advisable since many predacious insects pupate in the soil at the base of trees containing advanced broods of beetles, and by preventing the burning of debris around the stumps these insects are saved."

At times unusually dry weather during the early spring renders burning along the logs dangerous because of the fire hazard. Under these circumstances modifications in technique have been employed. Deep pits are excavated and the infested bark burned in the pits with comparative safety.

Except for sugar pines containing partial infestations along the bole, the method as described by Keen is fully applicable to all other infested trees. The trees in which only a fraction of the bole is infested have caused some difficulty, and often the practice has been to peel both the infested and green portions of the log. At other times green portions were left to be filled in by later attacks, and followed by a second treatment.

No established policy has been recognized or recorded, however, as to what should be done about the unattacked portions of the bole during initial control work. This is important and should be decided on as a matter of policy. The method which seems most feasible is to peel any green portions of the bole during the initial work, and not wait for a follow up control after the green portion has been attacked. The principal reason as shown by experience is that too often these trees are never again visited, and often if visited after the green areas are filled in by broods the fire hazard has prevented burning. Green portions of a log need only be peeled, and left unburned since no attacks are possible after the bark has been removed.

2. Sun-curing. This method, according to Patterson (18), "primarily consists of utilizing the sun's rays to attain such temperatures as are fatal to the broods of the beetle in or under the bark of infested logs. - -

It has been found that bark temperatures above 110° F. are necessary to cause death." The method is adapted to the control of bark beetle broods in thin bark tree species, such as lodgepole pine. Patterson states that "experiments have shown that the method is not applicable to trees that have thick bark, such as yellow pine and sugar pine, since the thickness of the bark of these trees acts as an insulator preventing the surface heat from reaching the beetle broods, which are either inside or under the bark."

3. Peeling-suncuring. The technique in applying this method is described by Keen (62): "Trees are felled across logs or other objects in order to hold them off the ground. They are then peeled throughout the infested length and the slabs or bark placed in an opening where they will receive the full rays of the sun during the middle of the day. Bark must be very carefully spread, and must not be in the shadow of other slabs or trees. On north slopes or in canyons it must be carried out to an opening or propped against rocks or trees, in order that the sun's rays may strike it at not less than a 45° angle. It can readily be seen that the method is tedious and requires great attention to detail, or it will fail to produce results."

Under the shaded conditions of a virgin forest the difficulties to be encountered in getting all sugar pine bark spread out in full sunlight are nearly insurmountable, and generally suncuring cannot be depended on as highly successful. It has been found to work best, however, in fairly open stands where the full force of the sun can penetrate exposed bark. In one project undertaken at Signal Peak in cutover reserve timber on the Sierra National Forest during August 1937 Struble (110) obtained successful results from 16 large trees treated by "felling, peeling and spreading the bark out so that the full force of the sun could strike it."

4. Peeling only. Peeling infested sugar pine logs to expose mountain pine beetle broods which lay between the bark and wood has been used with limited success during the dry season. This method was applied by CCC insect control crews working in Yosemite National Park from 1934 to 1939, but the results did not justify general recommendation of this method. Some of the reasons are evident from statements by Struble (115) who was closely associated with these projects. Doubt was expressed "as to whether summer control (peeling) is very effective, because of the variation in brood stages, some of which escape." In a project started "during the latter part of May and early part of June 1939 an attempt was made by the CCC insect control crew to control the 1938-1939 overwintering generations of the mountain pine beetle by felling and peeling. However, owing to the late start, a portion of the brood had already emerged and a portion was in the process of escaping. The control work at this time served in a good many instances to liberate adults and was thereby actually assisting them." One of the conclusions drawn from the results of summer control by peeling was that "the apparently small benefit derived from the treatment of summer broods does not seem justified. It is therefore recommended that summer control be suspended until such time as more efficient methods are developed, except for accessible trees that can be treated at the right time. Any attempt to carry on general control to reduce summer populations is impractical."

From the results obtained, mainly because of the large numbers of adults that are liberated by peeling and the continued development of more advanced brood stages, a considerable portion of which remain protected within the bark, this method of control is not recommended.

Chemical Control.

The search for improvements in methods of controlling bark beetle infestations led to developments in the chemical field. Some of the first experiments undertaken were based on the assumption that chemicals injected into the sap stream of newly infested trees might kill the insects and at the same time save the tree. Some tests of the effect of repellents were tried out, but the most promising development in this field was the application of penetrating oils to infested bark. Each method is discussed in order of importance.

1. Penetrating oils. The development of toxic penetrating oils followed shortly after a period of testing with fuel oils by N. N. Gay of the Standard Oil Company in cooperation with the Bureau of Entomology and Plant Quarantine in 1932. The objective of the burning tests was to cheapen the cost of control by eliminating peeling. However, as a result of close accounting of time kept on 19 ponderosa pines treated by spraying infested logs with fuel oils, Gay (46) concluded: "During periods of high fire hazard when the size of fire must be kept at a minimum, we believe that peeling the bark is cheaper, due to the fact that all the limbs cannot be utilized to generate heat and an exorbitant amount of oil will be required to effectively burn the bark." Consequently, further use of fuel oils was abandoned in favor of experiments to determine the effectiveness of penetrating toxic oils, applicable primarily during the summer season when it is too hazardous to burn.

Gay's (46) initial tests involved the use of 9 different oil formulae in separate experiments in which portions of an infested ponderosa pine tree were sprayed. From an examination of this tree 2½ months after spraying, Gay concluded: "that the oils that are effective are somewhat slow in action," and "that an oil such as Barrel House No. 21042R appears to offer some promise as a means of killing pine beetles without peeling the bark or going through a burning process."

Further tests of the most promising Standard oil formulae were continued by the Bureau of Entomology and Plant Quarantine from 1932 to 1935 to determine their possibilities in the control of western pine beetle in ponderosa pine, mountain pine beetle in sugar pine and lodgepole pine, flatheads (Melanophila californica) and Ips confusus. Most of the tests were made with formula 21046R (oil and naphthalene) and formula No. 22458R (oil and cresylic acid). As a consequence of considerable preliminary work with Standard Oil formulae, Salman (94) concluded: "It cannot be stated that any of the oils except 21046R showed promising results in these tests; for in all cases except when oil was used, the final emergence from the bark was as high or higher than a normal emergence."

Actual field tests of formulae #21046R and 22458R were undertaken by the Bureau of Entomology and Plant Quarantine in cooperation with the U. S.

Forest Service during the fall of 1933 to control bark beetles. The oils were applied by means of 4-gallon Smith-Banner pressure sprayers equipped with extensions and nozzles which fanned the oil into a fine spray. Regular crews of men were employed to fell, limb, pile the brush, and oil the infested logs.

Three small experimental projects were undertaken: (1) Bass Lake, Sierra National Forest, in which 39 ponderosa pine trees infested with D. brevicomis and flatheads were felled, limbed and oiled; (2) Dinkey unit, Sierra National Forest, in which 62 trees (ponderosa pine, sugar pine, Jeffrey pine) were felled, limbed and oiled; Tuolumne area, Stanislaus National Forest, in which 38 infested ponderosa pine and sugar pine trees were felled, limbed and oiled. In all, a total number of 139 infested trees containing broods of D. brevicomis, flatheads, D. monticolae, and D. jeffreyi were treated by spraying them with these oils.

The results of these oil control projects as reported by Struble (98, 100, 102), Patterson (80) and Buell (36) all indicated inconsistencies in amount of kill with variations from 0 to 96 percent. Such variations were in evidence in bark of the same thickness and treated with the same amount of oil (average of .024 gallons per square foot of bark area). It was also generally indicated that there was no correlation between amount of oil and amount of kill. All field tests showed that formula #21046R was very much more effective than #22458R.

Some of the reasons evident for inconsistencies in results and failure to kill were indicated from the reports of these projects. For example, in reporting the results of the Dinkey project, primarily concerned with D. monticolae in sugar pine, Struble (100) stated that "failure of oils was due in part to low temperatures existing at the time of application and continuing throughout the winter, and in part to lack of penetration through the bark." Patterson (80) reporting on the Tuolumne project cited low temperature, humidity, bark texture and thickness as the principal factors causing variation in results.

Experiments were continued during 1934 and 1935 by the Bureau in an attempt to overcome some of the difficulties which became apparent as a result of field control tests. New oil formulae were developed and applied; the effects of varying temperature and of constant temperature in relation to oil effectiveness were studied; studies were made of penetration in relation to bark texture; attempts were made to increase penetration by scoring the bark in different ways; and studies were undertaken to determine if bark beetle broods developed resistance to toxic oils.

In summing up the development of oil formulae, Salman (20) stated: "The best results were obtained with the following substances or mixtures: (1) Diesel oil of 27° A.P.I. gravity with crude flake naphthalene at the rate of three-fourths pound per gallon. It should be mixed while warm and should be protected from low temperatures. (2) Diesel oil (same grade as above) 2 parts, stainless creosote 1 part, lubricating oil, S.A.E. 30 viscosity, 1 part. (3) Diesel oil (same grade as above) with paradichlorobenzene at the rate of 45 grams per gallon."

Definite limitations in the use of toxic oils to control bark beetle broods beneath the thick bark of ponderosa pine and sugar pine were indicated from this work. In tests with sugar pines infested with D. monticolae Struble and Hensill (106) concluded: "Mature infested sugar pines cannot be treated effectively by oils unless the bark is removed and the inner surface sprayed or unless the outer bark surface is cut down to a thickness of $\frac{1}{2}$ inch." Working mainly with D. brevicomis Hensill (54) found that "it was impossible to obtain satisfactory control on the bottoms of logs unless the logs were rolled and the bottom half given a separate treatment from the top half." In studies of the effect of temperature, Struble (101) found that: "(a) An exposure of 1 week at temperatures between 70 and 90° F. produced the highest mortality of broods. (b) An exposure of 1 week to temperatures of 60 and 65° F. resulted in an appreciable reduction in mortality. Normal dosages produced from 55 to 58 percent kill. (c) No appreciable killing was found for either dosage at 50, 40 and 32° F. when exposed for a period of 1 week." Miller (67), studying the prolonged effect of a constant temperature of 60° F. in relation to oil treatment stated that the oil "reached its maximum effectiveness in a period of from 2 to 3 weeks. Prolonged exposures of more than 3 weeks at this temperature did not materially increase the brood mortality resulting from effects of the oil." Hensill's (55) studies of oil toxicity resulted in the observation that: "The various brood stages, of D. brevicomis in particular as well as D. monticolae, were found to have varying resistance. - - The order of resistance for both species was large larvae the most resistant, then medium larvae, small larvae, adults and pupae."

The results obtained, even with the most promising oil formulae developed, were extremely variable. Hensill (53) concluded that: "Although this method of bark beetle control may be desirable and could be used during the summer when the fire hazard is great, there are reasons why the use of this method is felt to be definitely limited. Because of certain factors which make it difficult to obtain consistent results the method cannot be generally recommended. Following are the factors which must be considered: the various bark characteristics, thickness, hardness and density; gravity, or the failure of oil to penetrate bark on the bottoms of logs due to run-off; temperature; brood stages and resistance; technique and applications." Salman (20) stated: "In addition, the difficulties concerned with the transportation of supplies in the forested areas of California and the high cost of the treatment as compared with the peeling-burning treatment limit its use and adaptability."

2. Tree Medication. Tree medication or tree injection as a control method has been limited in scope. The first attempts were undertaken by Patterson (78) who injected a few infested sugar pines near Jenny Creek, Oregon, with sodium arsenite in September 1927 to prevent attacks of the mountain pine beetle beneath the bark. This experiment was done in connection with similar but more detailed experiments to control broods of D. monticolae in lodgepole pine and D. brevicomis in ponderosa pine (Patterson, 75). Later injection experiments to kill D. monticolae broods in lodgepole pine, ponderosa pine, and white pine were reported by Gibson (47) and Bedard (33). Sodium arsenite and copper sulfate appeared to be most successful,

but in general all chemicals injected failed to reach the broods; they appeared to cause quick death and drying of tree tissue which in some cases was attributed as a partial cause of death to some of the broods.

Most of the experimental work with tree injection in sugar pine was done with one purpose--to save trees from aggressive D. monticolae attacks. The principle involved was to inject a chemical into the sap stream which would be distributed to cambium and phloem tissues without doing harm to these tissues, and at the same time kill or repel insects. The chemical was introduced by means of auger holes drilled on a tangent to the sapwood. The holes were connected by means of tubes to the container of solution on the outside. The solution entered the tree tissues by absorption through the living conductive tissue.

The manner in which mature sugar pines are attacked, section by section downward, indicated that injection might be employed to check the progress of invasion. The merits of injection if workable lay principally in the protection and saving of individual trees aesthetically valuable in park areas.

Experiments to test the possibilities of injecting sugar pines were undertaken by Gordon (49) in 1932 when D. monticolae infestations in sugar pine were epidemic. The initial injections were made in 18 small trees between 9 and 11 inches in diameter which were first attacked by the beetles through caging them on the trunks. Later tests were made on mature trees already attacked in the tops.

The most promising chemicals for injection experiments were indicated from Gordon's (49, 51) work in injecting white fir to prevent attacks of the fir engraver beetle. These were pyridine, picoline, lutidenes, halogens (potassium fluoride, potassium bromide, sodium chloride). All of these were tried on the small trees while pure pyridine, found to be the most promising chemical, was used in larger trees. Pure water was used in one small tree.

The results of this work as reported by Gordon (51) were not conclusive. He states: "The studies with pyridine show that fairly high concentrations are toxic to old foliage but not to the cambium or new growth. It was effective in killing the brood but did not prevent attack by the adults. Low quantities when injected were not toxic to the tree and only slightly so to the brood during the first 3 weeks after injection." Picoline and lutidenes "proved toxic to the cambium. They did not become well distributed in the cambium and were not carried to the foliage by the ascending stream." Concerning halogens, he stated: "One tree was injected with a weak solution of a mixture of the following salts: K_2F_2 , KBr, NaCl, (NaI?). The tree was injured; more than 50 percent of the foliage became discolored. The insect attack was not arrested." One tree injected with 15 gallons of water was found to have no effect on brood development.

As a final test of the effectiveness of pure pyridine in arresting the progress of D. monticolae attacks in the upper crown, Gordon injected a mature sugar pine (70 inches d.b.h.) located near the Grizzly Giant in Mariposa Grove, Yosemite National Park, early in September 1942. At the time of

injection 25 percent of the top part of the crown had faded sorrel. This tree was felled early in December the same year by control crews after the remainder of the crown had begun to fade. An examination of the bole showed that new attacks and eggs were distributed throughout the mid-bole from 20 feet above the base to within 50 feet of the top. Young active larvae were found toward the top. The chemical had in no way stopped the beetles from attacking.

The apparent failure of pyridine to check beetle attacks led to the development of tests with pure nicotine. Only one small experiment was undertaken to check D. monticolae in lodgepole pine, and because the results indicate possibilities in protecting sugar pines, they are mentioned here. This experiment, undertaken during 1934, involved 5 small lodgepole pines between 6 and 8 inches in diameter. Four of them were injected, 3 with 10 percent strength and one with concentrated strength. A fifth check tree was not injected. D. monticolae adults caged with these trees were found to attack the main trunk. Reporting on the results of this experiment, Struble (103) stated that "nearly 4 months after injection, no cambium injury was evident in any of the trees and no odor of nicotine could be detected. Needle injury was negligible. The attacks on all injected trees failed "to produce broods; "those on the check tree resulted in normal broods." Struble concluded: "These results indicate that nicotine may be of importance in hindering the progress and development of the mountain pine beetle. It did not repel adults or prevent them from making normal attacks and egg galleries."

3. Fumigation. The use of toxic gases to control bark beetle broods within the bark is a relatively new development. It was tried in a preliminary way by Yuill (123) during 1939 against D. monticolae in sugar pine and lodgepole pine, and D. brevicornis in ponderosa pine. Most of the tests were with sugar pine broods in logs. The gas used was methyl bromide because of its properties of diffusion and penetration through moist materials.

The tests undertaken by Yuill involved: (1) fumigation of logs within gas tight chambers; (2) fumigation of infested logs on the ground by introducing gas beneath a rubber fumigating blanket covering the log; and (3) fumigating infested logs on the ground by introducing gas beneath a blanket made from neoprene sheeting. The gas was introduced in measured quantities by means of a dispenser attached to 1-pound cans of methyl bromide. In the gas-tight chambers the gas was introduced in varying amounts for different tests, from 0.5 to 124 pounds per 1000 cubic feet of air space; in the logs covered by blankets the dosage varied from 4 to 51 pounds per 1000 cubic feet. The period varied from 24 to 48 hours.

Mortality results were 100 percent effective for D. brevicornis in loose ponderosa pine bark, and D. monticolae in sugar pine and lodgepole pine logs when confined in gas-tight chambers for 24 to 48 hours. The results beneath the rubber blanket were variable from 0 to 100 percent, but were generally poor because of the loss of gas through the blanket. The mortality in logs sealed beneath the neoprene blanket was 100 percent in all cases within 24 hours with 5 and 10-pound dosages per 1000 cubic feet.

As a result of this work, Yuill (123) concluded: "The results of these preliminary tests indicate that the use of methyl bromide has very definite possibilities for the control of bark beetles where intensive year round treatment is necessary and where the use of fire is undesirable. As yet we have no data on the expense of treatment where peeling is necessary. The cost of the fumigant itself is not excessive running not over \$0.35 per thousand feet BM of treated bole, and further tests may show much smaller dosages to be satisfactory. The principal short-comings of this method which have appeared so far are (1) fumigation of uninfested sections such as green butts probably will not preclude later attack and development of brood, and (2) the difficulty in making a gas tight fit of the blanket around the bole of the infested tree on excessively rocky or brushy ground limits the scope of usefulness."

Biological Control.

Native insect enemies have long been recognized as an element in the control of D. monticolae in sugar pine and D. brevicornis in ponderosa pine. The early observations of Miller (65) and Person (85, 89) and later observations and studies by Struble (99, 116), DeLeon (3, 4, 37, 39, 40), and Bedard (30) discussed previously give indications of the importance that is attached to beneficial insects. Likewise, in the institution of direct control practice, provisions for sparing the predators and parasites have been written into the instructions governing the burning method. For example, as previously mentioned, Keen (62) cautioned against burning around the stump so that the beneficial insects may be saved. This practice has been followed in connection with all large scale projects where the fell-peel-burn method was used. Except for the sparing of predators in ponderosa pine, it does no good in the control of overwintering D. monticolae in sugar pine since the clerids do not migrate to the bases of those trees until D. monticolae emergence is well under way and consequently they are destroyed.

The characteristic thick bark of sugar pine and ponderosa pine is a factor which limits decidedly the number of species of beneficial insects to be found. There are no parasites of any importance, except in the extreme tops where the bark is thin enough to permit oviposition. Thick bark is attractive mainly to the predator adults which find no difficulty in seeking out their prey or in establishing their predacious broods.

Experimental work to determine the importance of predators, particularly of Temnochila virescens Mann. and Thanasimus lecontei (Wolc.) as controlling agents of the western pine beetle, was undertaken by Person in 1922 and continued until 1930. As a result of these studies (87, 88, 90, 91, 92) an evaluation was obtained as to the relative importance of each one. T. lecontei and T. virescens were both considered very important among many lesser species, but of the 2 T. lecontei was judged most valuable on the basis of consistent populations, greater specificity to D. brevicornis as the principal host, and more uniform synchronization in life cycle with D. brevicornis. In actual experiments to test the effectiveness of T. lecontei as a controlling agent, Person (86) demonstrated "that clerids, under the conditions studied, are by far the most important insect enemy of the western pine beetle

Detailed studies and experiments were undertaken from 1937 to 1941 by Struble to determine the importance of predators in the control of D. monticolae in sugar pine, and also the possibility of increasing natural insect enemies. These investigations (21, 22, 23, 112, 113, 114, 117) were concerned mainly with the two insects most commonly associated with infestations of the mountain pine beetle, the green trogositid Temnochila virescens Mann. and the red bellied clerid Enoclerus sphegeus Lec. On the basis of quantitative abundance, both predators were judged approximately equal in importance, but each one in the larval stage was found to exert its influence separately on different seasonal broods of D. monticolae. For example, among 15 sugar pines containing overwintering infestations and 15 trees infested by summer broods, Struble (112) noted "almost complete absence of T. virescens larvae among overwintering broods" while among summer broods "E. sphegeus larvae were rarely found." Continued investigations (113) "established the fact that E. sphegeus is definitely associated with the overwintering larval brood and T. virescens with the summer broods."

The controlling action of adults and larvae of both species were studied. In separate controlled feeding tests the average daily consumption of D. monticolae adults by T. virescens adults during a 10-day period varied from .82 to 1.14; the average daily consumption by E. sphegeus adults during the same period was .83 D. monticolae adults (Struble, 112). Estimates of the controlling action of the larvae of each predator under field conditions indicated that T. virescens was more efficient than E. sphegeus. According to Struble (113) "the presence of T. virescens in numbers over 1.5 per square foot has an appreciable effect, while little effect was evident where as many as 5 E. sphegeus larvae per square foot were found."

In cage-controlled experiments with infested logs, the combined effectiveness of both adults and larvae of each predator were compared with checks from which the predators were excluded. The results of several duplicated tests showed positively, according to Struble (113) that T. virescens "destroyed between 80 and 91 percent of the D. monticolae brood by comparison with checks." (It must be noted, however, that at least part of the control exerted in these tests was probably due to the T. virescens adults in reducing the attacking D. monticolae adults before the latter had a chance to escape within the bark.) The control effectiveness of E. sphegeus in similar tests varied "from 0 to 20 percent in all tests," but this apparent failure according to Struble (113) was due to the "failure of E. sphegeus to become established under caged conditions."

The comparative efficiency of each predator was studied. The bases used in judging efficiency were: longevity of adults, fecundity, fertility, host adults and larvae destroyed, and length of life cycle. The highlights of this investigation (Struble, 113) were: (1) T. virescens adults live three times as long as E. sphegeus adults, (2) T. virescens lay six times as many eggs, (3) T. virescens eggs are higher in fertility than E. sphegeus eggs, (4) the number of host larvae and adults destroyed is from 2 to 3 times greater per individual for T. virescens, (5) the development period of larvae is 3 times greater for T. virescens than for E. sphegeus. On the basis of this investigation, Struble (113) concludes: "In all factors except length

of larval life, T. virescens appears to have a distinct advantage as a biological control agency over E. sphegeus. Consequently there is apt to be considerable mortality of brood from starvation unless they feed on associated insects under the bark, which is probably the case, or on new generations of the host developed lower down on the tree.

"Since both species have a one-year life cycle, neither one has a controlling advantage over the other from the standpoint of time. E. sphegeus loses considerable time in a long aestivation period of mature larvae before pupation. From the standpoint of predatory ability of larvae, T. virescens is almost 3 times as efficient as E. sphegeus. Therefore, it appears that even though T. virescens has a much longer larval life than E. sphegeus, it is active during this period and destroys many more host larvae. Where more than one generation of D. monticolae are developed in the same tree, which is commonly the case, it is possible for one T. virescens brood to work on both D. monticolae broods and thus increase their predatory efficiency."

Studies were made to determine the relative specificity for D. monticolae in preference to other hosts (Struble, 113). The results showed that T. virescens was far less specific than E. sphegeus, both from the standpoint of occurrence with other hosts and of number of individuals with any specific host. As a specific control agency, T. virescens was judged less reliable than E. sphegeus, although the latter species could not be considered entirely specific to D. monticolae. Both species also were found to be highly cannibalistic, showing no choice between host larvae and their own kind.

The possibilities of artificially propagating these predators to increase their number, and subsequently their efficiency in controlling D. monticolae, was investigated (Struble, 114, 23). Considerable experimentation was required before adequate technique was developed. One of the greatest difficulties to be encountered was in overcoming losses of predator larvae owing to cannibalism, and this was overcome only through the treatment individually of each larva.

The steps required in artificially rearing these predators were: (1) setting up of mating pairs of predators for oviposition, (2) collecting and incubation of eggs, (3) setting up individually each larva following hatching, (4) providing a satisfactory food supply, and (5) feeding the larvae. Eggs were obtained by inducing oviposition between the overlapping layers of crepe-paper spirals. The larvae, upon hatching, were placed individually in 1 dram pharmaceutical vials, each containing a thin layer of sawdust. Each larva was provided every 2 days with a D. monticolae larva. The host larvae were reared in logs under controlled rearing conditions.

The possibility of developing suitable substitute hosts was investigated, but was proven generally unsatisfactory because the mediums in which they were reared were unsuitable to the predator larvae. Furthermore, although some of the substitute hosts were satisfactory to T. virescens when transferred, they failed completely to be fed upon by E. sphegeus. The most promising among many substitute hosts tried were the larvae of the flesh fly Lucilia sericata Meig.

On natural scolytid host food, it was found possible to rear T. virescens and E. sphegeus from newly hatched larvae to adults. Struble (23) states that "out of 1,084 (T. virescens) larvae hatched in the summer of 1938 and reared on D. monticolae, 872 or 80 percent reached the adult stage, and all were fully formed." Concerning E. sphegeus he states that "out of 537 larvae hatched in the summer of 1938, only 174 or 32 percent reached the adult stage. Many of these were deformed and all were undersized, probably because this insect was unable to become adapted to the artificial environment."

In considering the possibilities of artificial propagation of native predators in the light of these investigations, Struble (23) concludes: "The cost of rearing these predators by use of their native hosts as food is much too high for practical purposes. Furthermore, the set-up of logs in which to rear the host is too cumbersome and is wasteful of green timber.

"The benefits to be derived by rearing great number of these predators are too uncertain to justify high rearing costs. Unless methods can be developed which will overcome these objections, there is little hope of increasing the beneficial effect of these predators beyond that of protecting them in nature."

Repellents.

Little experimentation has been done with repellents to prevent D. monticolae attacks on sugar pine, and the results have all been negative. The method used in each test of a given substance was to apply the substance to freshly cut green logs, and observe whether the substance would kill the beetles, trap them, or prevent them from attacking. The treated logs and checks in one test series were left in open shaded conditions where they would be exposed to attacks by beetles in flight; in the other, the beetles were forced to attack the logs.

One of the first tests was undertaken near Bass Lake in 1932 by N. N. Gay of the Standard Oil Research Laboratory, but the records were lost. The materials used, the methods of application and results are here reported from the memory of the writer who witnessed the experiment. As recalled, 8-foot sections of green sugar pine logs were used. To one of the sections was applied a $\frac{1}{4}$ inch coating of an asphalt compound, and to another a mixture containing Paris Green. A third compound, the constituents of which cannot be recalled, was tried on a third log. After a period of 6 weeks, all logs were peeled and it was found that all were attacked successfully regardless of material used. Fewer attacks were found on the log treated with asphalt than the others; the log sprayed with the mixture containing Paris Green showed no outstanding differences in concentration of attacks or of brood development in comparison with check sections.

In 1937 a few tests were made with a newly developed product called "Deadline." This was an extremely sticky compound developed by the California Spray Chemical Company. The tests were made under cage-controlled conditions using freshly cut ponderosa pine logs treated by an application of the sticky product. It was applied in diluted form by a fly sprayer. D. monticolae

adults were admitted to attack the logs thus treated and left for a period of 2 weeks between March 18 and 31, 1937, following which the logs were peeled and examined for attacks. In reporting the results, Struble (111) commented: "Most of the attacks were made on the sides of the logs in the bark crevices. A few entered the phloem at the cut surfaces. Well developed egg galleries were found, some containing eggs. It was apparent that as soon as a beetle began boring, the boring dust destroyed the effectiveness of the "Deadline," thus enabling the beetle to continue the attack unhampered. The difference in number of attacks on each log was apparently in no way influenced by the stickiness of the log, but more by chance selection according to light or some other factors."

DIRECT CONTROL RESULTS

Control work against infestations of the mountain pine beetle in sugar pine stands has been undertaken intermittently since 1913 by the fell-peel-burn method. In most instances this work has been in connection with projects involving the western pine beetle in ponderosa pine. Often there has been no separation by insects or tree species in these projects; however, the separations that have been made give us an indication of success as measured by a reduction in infestation following control work.

Most of the mountain pine beetle control projects were undertaken in the central Sierras from the Eldorado to the Sequoia National Forest. The largest projects were located in the Stanislaus National Forest, Yosemite National Park, and Sierra National Forest, and it is in these areas that the best evidence is available as to the success of direct control. Our judgment of success is based almost entirely on the results obtained in these areas where sugar pine stands attain optimum development. However, even at best there appears to have been no concrete evidence that the control work alone was entirely responsible for reduced infestations.

Contour Project.

One of the first bark beetle control projects in which sugar pine infestations were involved was the Contour Project instituted in 1913 on the Sierra National Forest. This project included all infestations (mainly D. brevicornis in ponderosa pine) between the 3,000 and 5,000 foot contour levels from the Merced River to the Kings River. This project, and also the Chiquito Basin project, were reported on by Ernest Dudley (43) in 1914, and their relative success was indicated in the statement that: "The control work of 1913 is not entirely satisfactory; probably not over 80 percent of the infestation in any locality has been destroyed."

Control work undertaken in 1914 on the Stevenson Creek project, Sierra, was directed primarily against D. monticolae in sugar pine. Writing of this project, Hopping (57) stated: "This area was badly infested in 1914. Control methods were applied in the spring of that year; 289 trees being cut and treated or an average of 82 trees to the section. Every tree which could be spotted as infested at the time of the work was treated. Subsequently, the trees killed later in the summer were numbered and the data collected which proved that 86.5 percent of the existing infestations at that time had been exterminated."

Bullock Project.

The Bullock project on the Stanislaus National Forest was undertaken from 1914 to 1916 to control primarily D. monticolae in sugar pine. This was a cooperative project in which the Yosemite Lumber Company, the White and Friant Lumber Company, and the U. S. Government participated. The area consisted of 14,080 acres of heavy virgin timber between the Merced and Tuolumne Rivers. According to Bachem and Welch (26) reporting for the lumber companies on the project, the volumes treated in 1916 were: sugar pine - 1,890,739 board feet; ponderosa pine - 147,669 board feet. In his annual report for 1917, Hopping (58) commenting on this project stated: "Examinations this year by J. M. Miller and W. E. Glendenning of the Bureau of Entomology reported that the infestation is so small as not to be worth working." In a statement to the lumber companies involved, Miller (64) stated: "It is fairly evident to any one who will carefully study the situation, both upon this tract and in the surrounding forests, that all the evidence which could be obtained in the spring season of 1917 pointed to a very marked decrease in the amount of infestation over that of the past 3 or 4 seasons. It is only fair to assume that the control work carried out in this region in recent few years contributed to this reduction. No prediction can be made, however, in regard to the length of time that the infestation will remain in the condition indicated in the spring of 1917. It may at any time increase."

Yosemite Projects 1918-1919.

During 1918 and 1919 control work was undertaken on 22,000 acres of ponderosa pine and sugar pine type in Yosemite National Park to control D. brevicornis and D. monticolae infestations. In commenting on this work, Patterson (74) stated: "The results of the control work of the first year were satisfactory in all areas except the Yosemite Valley, Unit #1. In this unit the recurring infestation amounted to 90 percent of the infestation treated in 1918. In all other areas the subsequent infestation of 1919 amounted to only 18 percent of the 1918 infestation. The volume of yellow pine and sugar pine timber saved the first year amounted to approximately 260,000 board feet. The percent of reduction in these areas the first year amounted to 86 percent."

Whiskey Creek Tract, Sierra.

Control work by the White and Friant Lumber Company to suppress infestations in sugar pine were undertaken between 1915 and 1917 on the Sand and Whiskey Creek tract. In commenting on the results, Miller (66) states: "Definite figures as to the results accomplished by this work are not available as no studies of the situation were undertaken. However, observations by those in touch with the areas indicate that a very appreciable reduction of losses was secured which persisted for several years after control work was discontinued."

One of the outstanding results of direct control of D. monticolae infestations was on the Whiskey Creek Tract undertaken in 1924. In a report of this project, Miller (66) stated: "It is evident that during 1922 and 1923

the infestation in the control area was progressing in step with that in the 3 check areas, as all 4 registered a decline from natural causes ranging from 20 percent to 57 percent. However, in 1924 all check areas registered an increase ranging from 84 percent to 199 percent while on the control area a decline of 84 percent occurred. This result was obviously due to the reduction of beetles within the area accomplished by the control work, as natural influences were apparently the same on all areas." These results together with previous information, according to Miller: "show rather conclusively that the mountain pine beetle responds more readily to the effects of control than the western pine beetle which attacks only yellow pine."

Control of Epidemics - 1931 to 1935.

The period between 1931 and 1935 was one of the worst on record for aggressive killing of sugar pines by D. monticolae and ponderosa pines by the western pine beetle in the central Sierra area. Many control projects were instituted and the results have provided a stronger basis for judging the effectiveness of direct suppression methods. A summary of some of these projects in which sugar pine was recorded separately from ponderosa pine is tabulated below.

Project	Location	Years of Treatment	Area acres	Reported by	Treated Trees	Sugar pine Volume b.m.
Yosemite	Yosemite NP	1933-34	8,605	Ernst (45)	427	2,127.04
Tuolumne	Stanislaus	1934	12,860	Patterson (81)	79	448.18
Buck Meadows	Stanislaus	1934	5,810	Malven (63)	48	124.02
Tuolumne NIRA	Stanislaus	1934	27,000	Patterson (82)	297	945.31
Jawbone	Stanislaus	1934	13,200	Parsons (71)	40	149.86

The results of these projects expressed in percentage reduction in infestation 1 or 2 years after each project, as compared with infestations at the time the project was started, include both pine species. Consequently there is no way to determine how effective the work was as applied against a given insect species. Ernst (45) reported that there was a 42 percent reduction in number of trees and a 61 percent reduction in volume. Patterson (83) reported a 66 percent reduction in the south Tuolumne project, a 72 percent reduction in the Buck Meadows area and an 85 percent reduction in the Jawbone area.

The apparent success of these projects is in contrast to the results obtained on the Pinecrest project, also reported by Patterson (83). He comments: "The 3 consecutive control projects that have been carried out on the Pinecrest recreational areas during the past 3 years (1933-34-35) have not, however, been so successful in ridding this area of persistent infestation in both ponderosa and sugar pine. It is very probable that the failure of these projects is partly due to the abnormal conditions encountered on areas of high recreational use; but in larger measure it is the result of the control work being confined exclusively to the main recreational area and leaving of untreated infestations on bordering areas."

On the Sierra National Forest no segregation was made between trees or insect species involved. Consequently, the estimates of direct control results are based on the reduction in number of infested trees regardless of species or insects involved. In reporting on the progress of the Sugar Pine Sale and Fence Meadow projects in 1933, Gustafson (52) stated: "This project was treated during the fall of 1931 and spring 1932. It was again treated during the fall of 1932 and spring of 1933. The work this spring included the areas of 1931 and 1932 and some additional acreage. Using the same areas as a check, we find a reduction in 1932 and 1933 infestations of 47 percent." In 1934 Munhall (70) made a comparison between infestations treated in 1933 and by subsequent maintenance control in 1934 on the Fence Meadow project. His figures are presented as follows:

<u>Year</u>	<u>Treated</u>	
	<u>Trees</u>	<u>Volume b.m.</u>
1933	1,438	4,333,000
1934	239	826,000

The decrease in 1934 over 1933 as shown by these figures is 85 percent in number of trees and 81 percent in volume.

The most recent project of any size involving sugar pine infestations was in the Shaver Lake-Big Creek area on the Sierra National Forest in 1941 and 1942. The area covered 9,200 acres in virgin type ponderosa pine and sugar pine. The infested trees on the area were treated in the spring 1941, and subsequently by maintenance work in the spring 1942. The results as reported by Spinney (96) indicated 90 percent control.

Discussion.

These various projects have nearly all indicated a marked reduction in infestation in from 1 to 2 years following direct control work. Consequently it appears that direct control by the fell-peel-burn method is successful, and we are bound to continue this practice unless it can be proven that success is more apparent than real.

One of the weaknesses in judging the effectiveness of these projects is the lack of adequate check areas in which to compare results with controlled areas. In all control projects undertaken, the objective has been to eliminate as many of the infested trees as possible over the entire infested unit, and thus eliminate the hazards to the living stand. The risks that might be involved because of untreated check areas ^{1/} could not be considered, and consequently it has never been possible to obtain the information needed to obtain a true evaluation of direct control results.

1/ The check areas used in comparing results on the Whiskey Creek tract, previously discussed, were at some distance removed from the controlled area and at lower elevations and on different sites. Because of this, it is doubtful that they could be considered as adequate check areas.

The question as to what would happen to an infestation if no control work were undertaken has been considered. There is too little evidence as yet to justify leaving D. monticolae infestations to run their course and be controlled by natural agencies. We do have some evidence that where no control was undertaken the infestations died out rather suddenly. One noteworthy example was reported by Salman (95) on the Lassen National Forest in 1939 in which groups of mature infested sugar pines appeared over a considerable area near Stirling City, causing losses estimated at over 300 board feet per acre. No control work was instituted, but in spite of this the infestation died out to a low endemic status by summer of the following year. There is no proof, however, that if control work were undertaken here the amount of loss would have been greatly lessened. Unless there is sufficient evidence to support leaving infestations to run their course without direct suppression, we must still continue to recommend and undertake direct control measures where great economic and recreational values are at stake.

Possibility of Improving on Direct Control Methods.

The development of sporadic infestations originating in windthrown trees and heavy slash was discussed in an earlier section. The number of localized D. monticolae outbreaks in sugar pine stands which are traceable directly to this source is perhaps far greater than any other, although no positive evidence was shown other than the association of windfalls themselves with the subsequent infestation. It would seem quite evident, therefore, that studies should be undertaken to find out first of all the importance of windfalls in building up sudden localized outbreaks in standing timber, and then attempt to control the infestations if it is found feasible to do so.

The control of windfall infestations would seem to offer more possibility of actual success in preventing localized D. monticolae outbreaks than the control of these infestations themselves after they have become established in standing timber. It would seem that control work exerted at this apparently most vulnerable point would pay dividends in the prevention of further losses. The field for improvement in direct control should therefore be pointed toward eradicating or preventing windfall infestations or those in heavy slash such as "long butts" or cull material left in connection with logging or right-of-way clearings.

There are 3 main reasons why the control of windthrow infestations alone has not been undertaken previously: (1) Most windfalls are blown down during the winter months, and do not become infested until the following spring or summer; some do not become infested until the following fall. (2) As discussed previously, summer control by peeling or sun-curing was not regarded as satisfactory. (3) The cost of peeling windfalls is high, and because of this there has never been any attempt to control infestations in these logs alone or to prevent them from being attacked. Frequently, however, windfalls have been peeled in connection with regular projects to control aggressive infestations in standing timber.

These reasons appear to be valid, but because there is so much evidence indicating that windfalls are a menace to living timber, we cannot afford to abandon the possibility of controlling infestations within them until more

information is obtained. If windfalls cannot be salvaged by hauling the logs to mills nearby, then either the D. monticolae infestations should be controlled or the logs should be treated in a manner to prevent them from being attacked.

The success of DDT in the control of so many different insects suggests the possibility that it may be used on windfalls, not only to prevent the establishment of broods but also to kill all the adults attempting to attack these green logs. The use of DDT as an emulsion sprayed on green logs if effective would be far less expensive than peeling these logs or the suppression of a subsequent aggressive attack on standing timber. There are also possibilities in the use of orthodichlorobenzene and fuel oil in combination to prevent attacks.

This field of investigative work on direct control is open and should be followed if we are to make progress toward eliminating a most important hazard.

POSSIBILITIES OF INDIRECT CONTROL

The basic purpose of indirect control is to reduce the insect hazard through timber management. To do this it is necessary to determine first of all what constitutes insect hazard, and having determined this to apply preventive methods which will fit in with good forestry practice. Stated in other words, indirect control is the practice of removing from the timbered stand insofar as possible all timber which on the basis of conclusive scientific data is known to be susceptible to beetle attacks. Thus, through the elimination of a favorable food supply the beetle is greatly handicapped in ability to build up destructive populations.

Western Pine Beetle.

The ideas that have been developed on indirect control apply principally to the western pine beetle in ponderosa pine. The first ideas stemmed from the direct approach in attempts to lure the beetle away from standing timber. This was done by felling green trees throughout a given area which because of their supposed attractiveness would absorb the adults in flight. Then by controlling the broods in these trap logs the menace to living timber would be eliminated. During the early 20's this idea was tested experimentally on the San Joaquin Project, the Southern Oregon-Northern California project, and the Antelope Project, but it was found to be relatively ineffective in reducing the beetle menace and was also wasteful of sound timber.

During the late 20's ideas of indirect control began to crystalize into a form that indicated hope for success. The western pine beetle was found to be selective in its habits of attack, particularly during endemic periods, preferring slow-growing, weakened or decadent trees to the more vigorous ones. Silviculturalists and entomologists undertook the study of tree characteristics and began classifications according to age and crown characters. A crown classification system based on age and crown vigor was developed by Dunning (6) for use in general marking practice in ponderosa

pine stands of the Sierra Nevadas. Greater refinements designed to facilitate recognition of beetle susceptible trees resulted in the Keen (13, 15) classification system and risk classes developed by Salman and Bongberg (20a).

The development of sanitation-salvage logging to control the western pine beetle by indirect means was the logical outgrowth of the recognition of differences in tree health and vigor and their relation to bark beetle attacks. Besides eliminating the beetle hazard and at the same time utilizing the timber, sanitation-salvage logging on an experimental basis in northeastern California and southern Oregon has for the past 7 years resulted in control effectiveness varying between 80 and 90 percent as compared with unlogged check areas. The details of the method, its application and results are discussed more fully by Keen and Salman (14a) and by Miller (69) in a summarization of studies on the western pine beetle.

Mountain Pine Beetle.

The success of the eastside indirect control work in reducing western pine beetle losses suggested possibilities of its application to control mountain pine beetle infestations in sugar pine. The dissimilarity between the 2 problems, both as to the habits of the insects involved, and the silvicultural aspects did not seem to present insurmountable obstacles in the way of a solution. Indirect control indeed offered so much toward the advancement of control methods in ponderosa pine that investigation of its possibilities in sugar pine could not be overlooked.

One of the first ideas to be investigated, as in the western pine beetle problem, was whether the mountain pine beetle was selective in its habits of attack. Studies of crown characteristics, age, diameter, growth rate, etc., and the possibility of a relationship with D. monticolae attacks were continued from 1941 to 1943. Eight distinct sugar pine crown types based on vigor and decadence were established and studied with respect to susceptibility. Crown class ratings developed for ponderosa pine by Dunning and by Keen were assigned to sugar pines wherever possible to determine if there was a relationship with susceptibility. The net result of this study by Struble (118, 119) discussed earlier so strongly indicated a lack in relationship between the various factors studied and beetle susceptibility that it seemed inadvisable to continue that approach. It emphasized the need for a more fundamental study both from the standpoint of the insect habits and of the host environment.

The study of beetle olfactory responses by use of the Gordon (50) olfactometer, discussed earlier, in a preliminary report by Struble (120) was an attempt to determine if there were marked differences in attractiveness between different tree substances; but no significant differences were found under the conditions of the experiments. The need for refinement in technique, permitting a more natural environment for the beetles in experiments of this kind, was indicated. However, because of the time that would be required and the uncertainty of securing desirable results this approach was discontinued.

Studies which were begun in 1943 and have been continued intermittently since then are concerned with the ecology of sugar pine and its relationship

to the mountain pine beetle. One phase is the relation of localized environment to the health or susceptibility of the individual tree. The other is the relation of general silvicultural and environmental factors to the health or susceptibility of a given stand. These studies have not gone far enough as yet to show how important host environment may be. However, as judged from beetle killed trees on certain areas observed, the greatest hazards appear to bear a closer relationship to maturity of stand and heavy stocking than to site quality. Greater losses in both volume and number of trees were found to occur on the best sites, but in every case these were associated with stand density and age.

The investigative work with the mountain pine beetle and its relation to attacks on sugar pine has not as yet provided a conclusive basis for embarking on indirect control as a solution to this problem. The main reason is that there appears to be a lack of selection of trees on any basis that can be recognized consistently. In the virgin stands, for example, over-maturity and incidence of mistletoe may be considered as high risk factors, but the attacks made also on healthy younger trees with vigorous crowns in these same uneven-aged stands minimize the importance of any factor that might be considered as high risk. The answer may be found as a result of the ecological studies under way.

In the light of present knowledge any attempts to reduce mountain pine beetle attacks in sugar pine by cutting of selected "high risk" trees appears to be of little avail. Furthermore, there are numerous examples of areas that have been cut on a Forest Service selective marking basis with the result that beetles have come in later to kill large numbers of thrifty "leave" trees. One reason for this appears to be that the opening of the stand increases the number of windfalls that occur later on, and as discussed earlier, windfalls are considered to be a primary source of infestation in living timber.

Only in second-growth stands that have come up since clear-cutting 20 to 40 years ago is the mountain pine beetle apparently a negligible problem. Except where there is heavy competition caused by the density of stems, these second-growth stands, particularly in the Yosemite-Sierra area, are relatively free from the menace of bark beetles. Such examples as there are would seem to offer evidence favoring clear cutting to remove the beetle hazard. However, such a drastic course cannot be advocated unless all attempts to remove the beetle hazard by other means fail to give the desired result.

CONTROL IN RELATION TO SILVICULTURE AND MANAGEMENT

The maintenance of sugar pine as a type species in the mixed coniferous forests in which it now occurs is a problem in forest management. What is decided eventually will rest with the relative timber values of all species as balanced against the cost of maintaining sugar pine in the stand. This latter problem is largely ecological and will remain with the silviculturists to decide.

The principal problem confronting forest entomologists at the present time and for some time in the future is the beetle menace in virgin stands. In the commercial forests the demands of the lumber industry are reducing these stands at a rapid rate; even so, it will be many years before they are out over completely. In park areas the sugar pine type forests will remain in their virgin state indefinitely. As long as these forests remain undisturbed from the effects of logging the hazard against insects is the same. The amount of protection that can be given in an effort to maintain losses at a low level will depend on the economic or aesthetic values to be preserved.

The amount and character of protection against bark beetles that can be given virgin stands still rests with the practice of direct control to suppress beetle populations. This practice must continue as a matter of policy to prevent undue losses until such time as other more effective control methods are found. So far, the fell-peel-burn method is the only one which is fully reliable, but its use is limited to the wet seasons. The possibility of improvement in methods and technique were indicated previously, particularly with regard to the treatment of windfalls and slash. Direct control is costly, but is fully justifiable on the basis of the protection to the living stand.

The marking and cutting that is done when commercial forests are slated for logging should be based on silvicultural technique. The overmature, decadent trees should be removed in most cases, even though they have not been found to bear a close relation to mountain pine beetle attacks because of the large volumes involved. What trees are removed in addition should depend on the silvicultural planning of the future stand. Great care should be exercised to prevent injury to roots and crowns of "leave" trees, since injuries serve as an attraction to the beetles in flight, resulting often in the death of these trees and a threat to others. The dangers resulting from beetles reared in heavy slash, discussed previously, should be removed by direct control methods.

The amount of protection against insects that can be afforded second growth sugar pine stands is dependent on the owner's timber management policy. The present Forest Service protection policy, particularly against fires, is conducive to the growth of dense white fir thickets which, according to silviculturists, overtower, suppress, and eventually kill out young sugar pines. Under such conditions sugar pine is destined to pass out of the picture in many areas unless competition from white fir is removed. Whether this is done will probably depend on future economic values of these two tree species. Silviculturists believe it is economically feasible to foster sugar pine as a dominant future crop only on the best sites which are conducive to its rapid growth. This will mean that the protection that is given against the insect menace to young stands will be limited to specific areas, and not to the total acreage which now includes sugar pine as a type species.

PUBLISHED REFERENCES

1. BETTS, H. S.
1944. Sugar Pine (*Pinus lambertiana*). American Woods. Forest Service, U.S.D.A. Washington, D. C. February.
- 1a. CRAIGHEAD, F. C., J. M. MILLER, J. C. EVENDEN, F. P. KEEN
1931. Control Work against Bark Beetles in Western Forests and an Appraisal of its Results. Jour. For. 29(7):1001-1018. November.
2. DE LEON, DONALD, W. D. BEDARD, T. T. TERRELL
1934. Recent Discoveries Concerning the Biology of the Mountain Pine Beetle and Their Effect on Control in Western White Pine Stands. Jour. For. 32(4):430-36. April
3. DE LEON, DONALD
1935. The Biology of *Coeloides dendroctoni* Cushman (Hymenoptera-Braconidae) an Important Parasite of the Mountain Pine Beetle (*D. monticolae* Hopk.). Ann. Ent. Soc. Amer. 28(4): 411-424.
4. _____
1935. A Study of *Medetera aldrichi* Wh. (Diptera-Dolichopodidae). A Predator of the Mountain Pine Beetle (*D. monticolae* Hopk., Coleoptera-Scolytidae). Entomologica Americana. 15 (new series) (2):59-91.
5. DOANE, R. W., E. C. VAN DYKE, W. J. CHAMBERLIN, AND H. E. BURKE
1836. Forest Insects. McGraw-Hill Book Co., Inc. New York and London.
6. DUNNING, DUNCAN.
1928. A Tree Classification for the Selection Forests of the Sierra Nevada. Jour. Agric. Res. 36(9). May
7. EVENDEN, J. C., W. D. BEDARD, AND G. R. STRUBLE
1943. The Mountain Pine Beetle, an Important Enemy of Western Pines. U.S.D.A. Circ. No. 664.
8. HOPKINS, A. D.
1899. Preliminary Report on the Insect Enemies of Forests in the Northwest. An Account of the Results Gained from a Reconnaissance Trip Made in the Spring and Early Summer of 1899. Bull. No. 21, New Series, U.S.D.A.
9. _____
1909 Practical Information on the Scolytid Beetles of North American Forests. I. Bark beetles of the Genus *Dendroctonus*. U.S.D.A. Bull. 83, Part I.
10. _____
1909 Contributions Toward a Monograph of the Scolytid Beetles. I. The Genus *Dendroctonus*. U.S.D.A., B.E. Tech. Ser. 17, Pt. 1.

11. HOPKINS, A. D.
1910. Insects which Kill Forest Trees. Character and Extent of Their Depredations and Methods of Control. U.S.D.A B.E. Circ. No. 125. November 25.
12. KEEN, F. P.
1928. Insect Enemies of California Pines and Their Control. State of Calif., Dept. of Natural Resources. Bull. No. 7.
13. _____
1936. Relative Susceptibility of Ponderosa Pines to Bark beetle Attack. Jour. For. 34(10). October
14. _____
1938. Insect Enemies of Western Forests. U.S.D.A. Misc. Publ. No. 273.
- 14a. KEEN, F. P. AND K. A. SALMAN
1942. Progress in Pine Beetle Control through Tree Selection. Jour. For. 40(11):854-858. November.
15. KEEN, F. P.
1943. Ponderosa Pine Tree Classes Redefined. Jour. For. 41(4) April.
16. MC KENZIE, H. L.
1941. Injury by Sugar Pine Matsucoccus Scale Resembles that of Blister Rust. Jour. For. 39(5):488-489.
17. MILLER, J. M.
1938. The Relation of Windfalls to Bark beetle Epidemics. Internat'l. Congress of Entom. II:992-1002.
18. PATTERSON, J. E.
1930. Control of the Mountain Pine Beetle in Lodgepole Pine by the Use of Solar Heat. U.S.D.A. Tech. Bull. No. 195.
19. PERSON, H. L.
1940. The Clerid Thanasimus Lecontei (Wolc.) as a Factor in the Control of the Western Pine Beetle. Jour. For. 38(5):390-96.
20. SALMAN, K. A.
1938. Recent Experiments with Penetrating Oil Sprays for the Control of Bark beetles. Jour. Econ. Ent. 31(1):119-123. Feb.
- 20a. SALMAN, K. A. AND J. W. BONGBERG.
1942. Logging High Risk Trees to Control Insects in the Pine Stands of Northeastern California. Jour. For. 40(7):533-39. July.
21. STRUBLE, G. R.
1941. External Sex Characters of Two Important Native Predators of the Mountain Pine Beetle in Sugar Pine. Pan-Pacific Entomologist. 17(4). October.

22. STRUBLE, G. R.
1942. Biology of Two Native Coleopterous Predators of the Mountain Pine Beetle in Sugar Pine. Pan-Pacific Entomologist. 18(3) July.
23. _____
1942. Laboratory Propagation of Two Predators of the Mountain Pine Beetle. Jour. Econ. Ent. 35(6):841. December
24. SWAINE, J. M.
1918. Canadian Bark Beetles. Part II. A Preliminary Classification, With an Account of the habits and means of Control. Bull. No. 14; Dom. of Canada, Dept. of Agric., Ent. Branch.
25. YUILL, J. S.
1941. Cold Hardiness of Two Species of Bark Beetles in California Forests. Jour. Econ. Ent. 34(5):702-709. October.

UNPUBLISHED REPORT REFERENCES

26. BACHEM, C. AND A. E. WELCH
1916. Cooperative White and Friant, Yosemite Lumber Company, U.S. Government. Insect Control in California, Season of 1916.
27. BEDARD, W. D.
1931. New Facts Regarding the Biology of the Mountain Pine Beetle in Western White Pine. Coeur d'Alene, Idaho.
29. _____
1933. Additional Information Concerning the Biology and Habits of the Mountain Pine Beetle in Western White Pine. Coeur d'Alene, Idaho.
30. _____
1933. The Relation of Parasites to the Mountain Pine Beetle Control in Western White Pine. Coeur d'Alene, Idaho.
31. _____
1937. A Study of Mountain Pine Beetle Infestations in Western White Pine. 1936 Investigations. Coeur d'Alene, Idaho.
32. _____
1938. A Study of Mountain Pine Beetle Infestations in Western White Pine. Coeur d'Alene, Idaho.
33. _____
1938. Tree Injection as a Control of the Mountain Pine Beetle in Western White Pine. 1938 Investigations. Coeur d'Alene, Id.
34. _____
1939. A Study of Mountain Pine Beetle Infestations in Western White Pine. Coeur d'Alene, Idaho.

35. BUCKHORN, W. J.
1944. Instructions for Making Bark beetle Surveys in the Virgin Ponderosa Pine Stands of Oregon and Washington. Portland, Oregon.
36. BUELL, CRAWFORD R.
1933. Insect Control Report Sierra National Forest. Fence Meadow Project (Dinkey Unit). North Fork, Calif.
37. DE LEON, DONALD
1929. Introductory Study of the Parasites, Predators and some other Associated Insects of the Mountain Pine Beetle in Lodgepole Pine. Coeur d'Alene, Idaho.
38. _____
1930. Notes on the Emergence and Sex Ratio of the Attacking Parent Adults of *Dendroctonus monticolae* in White Pine. Coeur d'Alene, Idaho.
39. _____
1930. The Parasites, Predators, and Associated Insects of the Mountain Pine Beetle in lodgepole Pine. Coeur d'Alene, Id.
40. _____
1931. The Important Parasites, Predators and Associated Insects of the Mountain Pine Beetle in Western White Pine. Coeur d'Alene, Idaho.
41. _____
1931. An Annotated List of the Fauna Associated with the Mountain Pine Beetle in Western White Pine. Coeur d'Alene, Idaho.
42. _____
1935. Forest Insects of the California National Parks. Part I - Insects Affecting Sugar and Ponderosa Pine. N. P. S. Field Division of Forestry.
43. DUDLEY, ERNEST
1914. Contour and Chiquito Projects - Sierra Nat'l Forest, March 10 to May 23, 1914. North Fork, Calif.
44. EVENDEN, JAMES C.
1933. Host Selection in Relation to the Control of Bark Beetles. Coeur d'Alene, Idaho.
45. ERNST, EMIL
1934. Report of Insect Control, Spring of 1934. Yosemite Nat'l Park, Calif.
46. GAY, N. N.
1932. Pine Beetle Problem. Research and Development Department. Richmond, Calif.

47. GIBSON, A. L.
1928. Investigations of Mountain Pine Beetle in Lodgepole Pine and Yellow Pine (Progress Report No. 2). Coeur d'Alene, Id.
48. _____
1931. The Mountain Pine Beetle in Western White Pine. 1930 Progress Report. Coeur d'Alene, Idaho.
49. GORDON, A.
1932. Tree Injection Experiments in White Fir and Ecological Studies of Insects Attacking Yellow Pine. Season of 1931. Berkeley, Calif.
50. _____
1933. Apparatus used in a Study of the Western Pine Beetle. Berkeley, Calif.
51. _____
1933. Tree Medication Experiments on the Control of the Fir Engraver Beetle. Berkeley, Calif.
52. GUSTAFSON, CARL A.
1933. Insect Control Report Sierra National Forest. Fence Meadow and Sugar Pine Sale Projects. North Fork, Calif.
53. HENSILL, G. S.
1935. Review of Oil Control Experiments on Pine Bark Beetles. Berkeley, Calif.
54. _____
1935. Some Final Field Experiments on Oil Control of Pine Bark Beetles. Berkeley, Calif.
55. _____
1935. Summary of Laboratory Experiments and Toxicity Tests Concerned with Oil Control of Pine Bark Beetles. Berkeley, Calif.
56. _____
1936. Some Olfactory Responses of the Mountain Pine Beetle, *Dendroctonus monticolae* Hopk. Berkeley, Calif.
57. HOPPING, RALPH
1916. Inspection Report Stevenson Creek Project. North Fork, Calif.
58. _____
1917. Annual Report. Bullock Project.
59. JOHNSON, P. C.
1936. Field Manual of Bark beetle survey methods, California Region. Berkeley, Calif.

60. KEEN, F. P.
1916. Report #12. Selection Principle Experiments with *Dendroctonus monticolae*. Project 15a, Ashland Area Lamb's Mine Unit.
61. _____
1916. Report #4. Seasonal History of *D. monticolae*. Project 15a. Ashland Area--Lamb's Mine Unit.
62. _____
1927. Manual of Bark beetle control in Western Pine Forests. U.S.D.A., Forest Service. Mimeo. Circ.
63. MALVEN, STEVEN ST. J.
1934. Insect Control Project Stanislaus National Forest. Buck Meadows Unit. Sonora, Calif.
64. MILLER, J. M.
1917. Statement to the White and Friant Lumber Company and the Yosemite Lumber Company regarding tract of timber between the Merced and Tuolumne Rivers near El Portal, Calif. Ashland, Oregon
65. _____
1918. Factors in Natural Control of the Mountain Pine Beetle, *Dendroctonus monticolae* Hopk. Ashland, Oregon.
66. _____
1926. Results on the 1924 Insect Control Work on the Whiskey Cr. Tract, Season of 1924. Stanford University, Calif.
67. _____
1934. Effectiveness of Pine Beetle Oil #21046R in Relation to Time at a Constant Temperature of 60° F. Berkeley, Calif.
68. _____, G. R. STRUBLE AND R. O. HALL
1944. A Review of Forest Insect Control and Investigations on the Sierra National Forest, 1909--1943. Berkeley, Calif.
69. _____
1945. Biology and Control of the Western Pine Beetle. Summary of Investigations and Control Work.
70. MUNHALL, J. K.
1934. Insect Control Fence Meadow Project Sierra 1934. Memo. to Forest Supervisor, North Fork, Calif.
71. PARSONS, BERT E.
1934. Jawbone Insect Control Project, Stanislaus Nat'l Forest. Sonora, Calif.

72. PATTERSON, J. E.
1917. Memorandum for Dr. A. D. Hopkins: Notes on the Overwintered Broods of *D. monticolae* Hopk. in Lodgepole Pine. Yosemite National Park, Calif.
73. _____
1917. Memorandum for Dr. A. D. Hopkins: Account of the Attack and Mating--in Yosemite National Park, California, during August 1917.
74. _____
1923. History and Review Yosemite Park Control Project, 1918 and 19 Ashland, Oregon.
75. _____
1927. Progress Report of the Studies of the Mountain Pine Beetle Season of 1926. Stanford University, Calif.
76. _____
1927. Studies of the Mountain Pine Beetle, *Dendroctonus monticolae*, in Lodgepole Pine Infestations. Season of 1926. Stanford University, Calif.
77. _____
1928. Studies of the Mountain Pine Beetle in Lodgepole Pine and Other Studies Conducted in Southern Oregon in 1927. Stanford University, Calif.
78. _____
1928. Experiments with the Mountain Pine Beetle in the Prevention of Attacks and Killing of Broods. Stanford Univ., Calif.
79. _____
1934. Epidemic of *Dendroctonus monticolae* Resulting from Broods Breeding in Sugar Pine Slash--Big Creek Basin, Stanislaus National Forest, California. Berkeley, Calif.
80. _____
1934. Preliminary Results of Oil Treatment of Ponderosa Pine Infested with *D. brevicornis*, and of Sugar Pine Infested with *D. monticolae*. ECW Field Studies, Stanislaus Nat'l Forest. Berkeley, Calif.
81. _____
1934. Second Progress report on Tuolumne Insect Control Project. Berkeley, Calif.
82. _____
1934. Report of Stanislaus Tuolumne NIRA Insect Control Project, Stanislaus National Forest, California. Berkeley, Calif.
83. _____
1935. Forest Insect Surveys, Stanislaus National Forest. Season of 1935. Berkeley, Calif.

84. PATTERSON, J. E.
1935. Forest Insect Problems of the Yosemite National Park. Berkeley, Calif.
85. PERSON, H. L.
1922. Preliminary Studies on Predacious Insect Enemies of *D. brevicomis*. North Fork, Calif.
86. _____
1922. A Study of the Predacious Insect Enemies of the Western Forest Scolytids. Preliminary Report. North Fork, Calif.
87. _____
1924. A Quantitative Study of *D. brevicomis* Broods, Their Mortality, the Effect of Predators and Emergence Periods for *D. brevicomis* and *T. nigriventris*. North Fork, Calif.
88. _____
1924. Further Studies on the Predacious Insect Enemies of *Dendroctonus brevicomis*. Klamath Falls, Oregon. North Fork, Calif.
89. _____
1928. A Study of the Clerid, *Thanasimus nigriventris* Lec., with Notes on Other Insect Enemies of the Western Pine Bark Beetle. Stanford University, Calif.
90. _____
1928. Western Pine Beetle Biological Studies, Modoc National Forest. Season of 1928. Berkeley, Calif.
91. _____
1929. Biological Control Studies with the Western Pine Beetle--Progress Report 1929. Berkeley, Calif.
92. _____
1930. Studies in the Biological Control of the Western Pine Beetle, *Dendroctonus brevicomis* Lec. Berkeley, Calif.
93. RUST, HENRY J.
1930. Relation of Insectivorous Birds to the Mortality of the Mountain Pine Beetle during the Flight Period. Coeur d'Alene, Idaho.
94. SALMAN, K. A.
1933. Further Tests of Oil Sprays to Control the Western and Mountain Pine Beetles. Berkeley, Calif.
95. _____
1939. Reconnaissance of Westside Infestation conditions, Season of 1939. Berkeley, Calif.
96. SPINNEY, W. W.
1941. Insect Control Report Sierra. Big Creek Project. North Fork, Calif.

97. STRUBLE, G. R.
1933. Mortality of *D. monticolae* Hopk. Larvae due to Low Temperatures. Berkeley, Calif.
98. _____
1933. Preliminary Results of Oil Treated Ponderosa Pine Infested by *D. brevicornis* and *Melanophila gentilis*. Berkeley, Cal.
- * 99. _____
1934. The Mountain Pine Beetle in Sugar Pine, Season of 1933. Preliminary Report. Berkeley, Calif.
100. _____
1934. Summary of results, Dinkey Oil Control Project 1933. Berkeley, Calif.
101. _____
1934. Relation between Temperature and Effectiveness of Pine Bark Oil Formula 21046R on *D. brevicornis* broods. Berkeley, Cal.
102. _____
1934. Final Mortality results of Oil Treated Ponderosa Pine Infested by *D. brevicornis* and *M. gentilis*. Berkeley, Calif.
103. _____
1934. Nicotine Injection of Lodgepole Pine in Relation to Mountain Pine Beetle Attacks. Berkeley, Calif.
- * 104. _____
1935. The Mountain Pine Beetle in Sugar Pine, Season of 1934. Berkeley, Calif.
- * 105. _____
1935. Some Recent Studies of Host Selection by the Mountain Pine Beetle in the California Region. Berkeley, Calif.
106. _____ and G. S. HENSILL
1935. Oil Control Experiments Directed against *D. brevicornis*, *D. monticolae* and Flatheads, Season of 1934. Berkeley, Cal.
107. _____
1936. Studies on the Nutritional Requirements of Mountain Pine Beetle Larvae. Berkeley, Calif.
108. _____
1937. Laboratory Memorandum. Number of *D. monticolae* Ecdyses and period of each instar. Berkeley, Calif.
109. _____
1937. Nutritional Requirements of *Dendroctonus monticolae* Hopk. The Development of Rearing Equipment and Experimental Technic. Progress Report. Berkeley, Calif.

110. STRUBLE, G. R.
1937. Signal Peak Insect Control Project, Sierra National Forest. Berkeley, Calif.
111. _____
1937. "Deadline" as a Protection Against *Dendroctonus monticolae* Attacks. Laboratory memo. Berkeley, Calif.
112. _____
1938. *Temnochila virescens* and *Enoclerus sphegeus* in Relation to the Mountain Pine Beetle in Sugar Pine. Berkeley, Calif.
113. _____
1939. The Green Trogositid and Red Bellied Clerid in Relation to the Control of the Mountain Pine Beetle in Sugar Pine. Progress Report. Berkeley, Calif.
114. _____
1939. Artificial Propagation of two Native Predators of the Mountain Pine Beetle in Sugar Pine. Berkeley, Calif.
115. _____
1939. Status of the Mountain Pine Beetle in Mariposa Grove and Recommendations for Control. Berkeley, Calif.
116. _____
1940. The Habits and Control of the Mountain Pine Beetle in Sugar Pine. Berkeley, Calif. (Manuscript suppressed)
117. _____
1940. Native Predators of the Mountain Pine Beetle in Sugar Pine. Progress report, Season of 1939. Berkeley, Calif.
118. _____
1942. Crown Decadence of Sugar Pine in Relation to Attacks by the Mountain Pine Beetle. Preliminary Report. Berkeley, Calif.
119. _____
1942. Growth Rate of Sugar Pine in Relation to Attacks by the Mountain Pine Beetle. Preliminary Report. Berkeley, Calif.
120. _____
1944. Preliminary Results of the Olfactory Responses of the Mountain Pine Beetle, Season of 1943. Berkeley, Calif.
121. TERRELL, T. T.
1933. The Flights or Dissemination of Forest Insects. Coeur d'Alene, Idaho.
- 121a. WHITESIDE, J. M.
1935. Temperature Requirements for Pupation of the Western Pine and Mountain Pine Beetles. Berkeley, Calif.

122. YUILL, J. S.

1937. Low Lethal Temperatures Affecting the Mountain Pine Beetle,
1927-1936. Berkeley, Calif.

123.

1940. Preliminary Tests of Fumigants (Methyl Bromide) in Bark
beetle Control. Season of 1939. Berkeley, Calif.